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# Biogeography: Its History and Continuing Relevance to Paleoanthropology

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# BIOGEOGRAPHY:
# ITS HISTORY AND CONTINUING RELEVANCE TO PALEOANTHROPOLOGY

by

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Biogeography figured prominently in the formation of the modern natural sciences and played a crucial role in Darwin's theory of natural selection. However, as an avenue of investigation, biogeography remained underdeveloped until the last half of the twentieth century when the scientific community at large accepted the legitimacy of plate tectonics. The investigation of the spatial and temporal distribution of life on earth was finally conjoined with investigations of earth's geological history. Paleoanthropologists have long been focused on the spatial and temporal distribution of hominin species on the African landscape and beyond. As biogeographers have continued to refine their methods, particularly with regard to cladistic analyses, paleoanthropologists can potentially gain new insight into the evolutionary history of *Homo sapiens*.

***Preface:***

What are the details of our evolutionary genealogy? Did our earliest hominin ancestors arise in East Africa? South Africa? —or elsewhere? Were two of the earliest hominins, *Australopithecus afarensis and A. africanus*, distinct eastern and southern African species respectively (Johanson, et a., 1978)? —or, were they simply regional variants of the same species (Tobias, 1980)? Can we make similar distinctions between the eastern and southern robust australopiths (*Paranthropus boisei* and *P. robustus*, respectively)? How do we connect the historical dots between derived contemporary forms? *P. boisei*, with its massive cranio-facial features, stood in stark contrast to the tall and gracile *H. erectus*. What is the significance of their coexistence on the African landscape (Tattersall, 2009)?

Paleoanthropologists have been driven by basic questions such as these since the early twentieth century when Marcellin Boule (1911-1913) reconstructed Neanderthals as monstrous brutes (Trinkhaus, 1985) and Raymond Dart (1925) offered the Taung Child as weighty evidence for bipedalism in our ancient, ape-like ancestors. Through the years, questions regarding the complex roots of our hominin ancestry have often provoked fierce debates—to be expected for a subject as intrinsically personal and grandiose as the deep origins of humankind (see Tattersall, 2009 for discussion).

Nonetheless, evidence has been gathered through decades of inquiry, enabling scientists to begin piecing together the genealogical history of our hominin ancestors. One of the pertinent questions that has emerged concerns the spatial and temporal dynamics of hominin distribution both within and beyond Africa. Particularly, a desire to understand the manner in which early hominins moved and speciated across the African continent has inspired much research (e.g. see *African Biogeography, Climate Change, & Human Evolution* (Bromage and Schrenk, editors, 1999)).

African hominin fossil sites are clustered in two distinct regions, commonly defined as eastern and southern Africa. The biotic relationship between the two regions is pertinent to the understanding of human origins as the fossil record indicates the continuous hominin occupation of both dating back almost three million years (Klein 1999). While the two regions are believed to have been relatively isolated throughout much of hominin history, direct connection between the two undoubtedly existed at least periodically. In fact, uncovering the nature of those connections has been a platform for investigation for many paleoanthropologists. Alan Turner

and Bernard Wood (1993), for example, sought to uncover the spatio-temporal history of the eastern and southern species of robust australopith. One of the major debates at the time concerned the legitimacy of placing these hominins in a shared and unique genus, *Paranthropus*. The main question concerned whether or not *P. robustus* and *P. boisei* shared a direct common ancestor (monophyly), or whether evidence suggested that they had evolved independently from one another and stemmed from southern and eastern variants of *Australopithecus* (implying paraphyly).

By looking at the biogeography of the robust australopiths in the context of the broad biogeographical patterns of other contemporary fauna, Turner and Wood (1993) argued for monophyly and the legitimacy of the paranthropine clade. Citing the monophyly of other faunal groups with eastern and southern African members as evidence, Turner and Wood (1993) supported a scenario in which a common East African paranthropine ancestor (*P. aethiopicus*) gave rise to the southern and eastern variants of the genus. This study remains a seminal example of the application of biogeography to the study of hominins. As such, similar biogeographical investigations pertinent to hominin distributional history soon followed (e.g. Bromage et al., 1995; Bromage and Schrenk, 1995; Grubb et al., 1999; Strait and Wood, 1999). For instance, Grubb et al. (1999) closely examined the large mammalian fossils found within and between eastern and southern Africa as a means to expose more precise regional faunal variations beyond the "East-South" dichotomy. They uncovered a spectrum of discrete but overlapping regional faunas containing many species with widespread distributions—evidence for a more complex biotic relationship between the eastern and southern sections of the continent.

In this regard, paleoanthropologists have worked within the biogeographical paradigm. In order to understand the distributional and genealogical patterns of hominins, researchers have turned their attention to the manner in which they were situated within the greater context of their ecological settings. Though much work has been done, the insight offered by biogeographical interpretations has only just begun to be applied to the study of paleoanthropology. In the following pages I hope to convey the potential for further studies of hominin biogeography through the application of new methods and fresh approaches to long-standing paleoanthropological questions.

CONTENTS

TABLES

Table

FIGURES

Figure

## Chapter 1: Introduction

The non-random distribution of life on earth is readily apparent to those who study the natural world. Indeed, the fact that plants and animals adhere to specific environments, patterning themselves accordingly across landscapes, has long been recognized (Aristotle, 350 B.C.E.; Linnaeus, 1744; Buffon, 1749; Candolle 1820; Hooker, 1853; Sclater, 1858; Darwin, 1859). However, understanding the environmental context of biotic distribution is only half of the story. The biogeographers who concern themselves with the geographical distribution of life on earth seek an understanding that is both spatially and temporally more complex, belying the elegant simplicity of biogeography's central question: why do organisms exist where they do and how did they get there? The elaborate natural systems that biogeographers seek to comprehend are fundamental to a holistic understanding of natural history, and as such, biogeographical concepts have remained a relevant and rewarding avenue of inquiry since the dawn of the natural sciences.

Ironically, though biogeography holds central significance to a wide range of academic research, as a discipline it can be maddeningly amorphous and difficult to define—university departments of biogeography are few and far between (Morrone, 2009; Parenti and Ebach, 2009; Schuh and Brower, 2009). Nonetheless, natural science departments of all stripes are filled with biogeographers, explicitly self-described or not. Any naturalist that notes, for example, a particular species of monkey living in a given forest is effectively cataloging biogeographical data. In a very real sense, this lack of academic cohesion among biogeographers has resulted in the historically fractured and contentious nature of the discipline. Thankfully, in the last decade or so, a concerted effort has been made to forge a cohesive notion of what biogeography seeks to

interpret, and more importantly, how it proposes to go about doing so (Morrone, 2009; Parenti and Ebach, 2009; Schuh and Brower, 2009).

Biogeography has a rich and influential history in science. Charles Darwin (1859) dedicated no less than two chapters of *The Origin of Species* to elucidating the biogeographical scaffolding with which his theory of natural selection was built. Notions of life's biogeographical patterns were central to the ways in which enlightenment thinkers sought to scientifically reframe the natural world. Yet, as alluded to, would-be biogeographers have spent much time and energy attacking opposing methodologies and proclaiming the primacy of their own particular theoretical frameworks (Morrone, 2009). As a result, there remains a dizzying array of biogeographical sub-disciplines—each with its own self-identifying coinage (see footnote in chapter three for a partial list). Because of this, a foray into the "biogeographical" literature quickly reveals a confusing diversity of concepts and approaches.

Nevertheless, as one might expect, particular methodologies are often best suited for particular questions and more than anything else, this is the resolution which modern biogeographers are beginning to accept amongst themselves. In this regard, biogeography's application to any given field of research is going to manifest itself in ways best suited to the parameters inherent to that particular discipline. Every academic field is characterized by its own sets of data, its own stated goals, and its own strengths and weaknesses. If nothing else, the potential pool of subject material for the biogeographer is unimaginably immense and to assume a one-size-fits-all approach is counterintuitive. For example, many of the original, concerted efforts at biogeographical interpretation focused on the plant distributions across the continents. Without a doubt, phytogeography is invaluable to our understanding of general biotic history, but to propose that plants and animals, for instance, do not have nuanced differences in their

evolutionary and biogeographical mechanics is shortsighted. Similarly, marine organisms have been the focus of countless biogeographical studies, and though certainly pertinent, the relevance of their biogeographical interpretations to land-based organisms is perhaps tangential at best. Also, the temporal and spatial scales of the biogeographical puzzles that a researcher seeks to solve have and immense impact on the applicability of certain methods and theories.

In this essay I hope to convey the great promise that biogeography holds as a discipline in light of recent advances in quantitative methods and an emerging sense of cooperation among many of its practitioners. Particularly, I hope to convey the ways in which biogeography can be applied to the study of human evolutionary history in order to gain novel insight into our hominin ancestors. This is not to suggest that paleoanthropologists have ignored biogeographical approaches in the past—quite the contrary. I merely wish to propose that biogeography has rapidly evolved as a science over the last several decades and that perhaps it is time for paleoanthropologists to reevaluate past biogeographical studies in light of new methods and theories emerging from other corners of the academy.

In the following pages I will give a brief history of biogeography as a discipline and describe the recent advances in its field of study. Because of the enormous breadth of material that can be potentially covered, my treatment of the subject in this format is selective. I focus on a subset of biogeographical concepts and studies that I feel are most pertinent to future research in paleoanthropology. For one, I do not delve deeply into the phytogeographical studies that are well represented in the biogeographical literature and have obvious pertinence to the study of hominin evolution (see Owen-Smith, 1999). Instead, I focus on the better known and more rigorously debated faunal studies that have been applied to paleoanthropological questions in the past.

For obvious reasons, the study of human evolutionary history is arguably the most personal of endeavors for the natural historian. At the risk of overt anthropocentrism, it is difficult to deny that the unique biological position that humanity occupies on this earth gives added weight to questions regarding how and why we evolved into the sentient beings that we are today. While we are undoubtedly a part of the natural world, we also stand apart from it in many profound ways. No other organism has complex language, complex culture, and civilization. No other living creature has the capacity to reshape, degrade, and pollute the world on a global scale. No other life form has catapulted itself beyond the confines of earth's gravity and atmosphere. Yet, all of these capabilities are relatively recent in origin. Our biological beginnings were no different than those of any other creature, and the confluence of evolutionary events that allowed for the emergence of *Homo sapiens* is the central puzzle around which the research of paleoanthropologists is designed. Clearly, the biogeographical context within which hominins evolved is a crucial piece to understanding that puzzle.

## **Chapter 2**: **Biogeography and the Natural Sciences**

One of the many cognitive leaps made by Enlightenment thinkers was to question the long held belief in a static natural world. The founders of modern science began to carefully examine the intricacies of natural systems and contrast their observations against the theologically inspired explanations of the past (Kant, 1784). Eventually, the notion of an earth fixed in heavenly order could not withstand the weight of empirical inquiry, thus emerging a dramatic paradigm that continues to serve as the backbone of the natural sciences. The earth, far from being static, is as vast as it is dynamic. Intrinsic to the 18th century vision of a variable and flexible natural world were the emerging hypotheses regarding the observable distribution of flora and fauna across the globe, or what we now refer to as biogeography.

This is not to say that theological influence was at once starkly removed from biogeographical interpretation. In *Oratio de Telluris Habitabilis* (1744), Carl Linnaeus explicitly utilized the book of Genesis to forge one of the original biogeographical concepts: a finite center of origin from which species disperse. Quite elegantly, Linnaeus postulated that as the floodwaters of the great deluge receded and re-exposed the land, the Noachian cargo spread to all corners of the world with each species dispersing to areas with suitable habitats (Linnaeus, 1744). In conjunction, Linnaeus (1781) also contended that God's original site of creation, Eden, was an island at the earth's equator with a "lofty mountain adorning its beautiful plains" (p. 90). This topography allowed for all possible habitats—from tropical forest to snow-capped mountaintop—to be accounted for by God's original design. The Linnaean explanation for modern faunal distributions rested on the assertion that each particular habitat type, regardless of its geographical location, will contain more or less the identical fauna that occupied the equivalent habitat in Paradise. While it is easy to disparage Linnaeus for neglecting to actually

compare the fauna in similar but discrete habitats, he was obviously much more concerned with the systematics of the natural world than with its ecological complexities. Regardless, he was undoubtedly the first to suggest the center of origin/dispersal explanation for biological distributions, an explanation that continues to be utilized to this day (Nelson & Platnick, 1981).

Ultimately, a contemporary of Linnaeus did eventually examine the facts on the ground. In his seminal work, *Histoire Naturelle, Générale et Particulière* (1749), Georges Leclerc, Compte de Buffon, presented evidence demonstrating that Linnaeus' post-diluvium explanation for the distribution of life on earth simply did not hold water. Buffon rightly agreed that species adhere to environments for which they are designed, but also made the prescient observation that geographically isolated tropical locations with similar environmental characteristics contained fundamentally different mammalian populations (Buffon, 1749; 1761). In fact, the presence of wholly different species populations in similar, but geographically isolated environments is now simply referred to as "Buffon's law". Thus, empirical evidence effectively required that Buffon remake the Linnaean distribution model. In order to account for the undeniable faunal differences between the continents, Buffon proposed that fundamental morphological changes must occur in organisms as they venture further away from their ancestral habitats and begin to encounter novel environmental conditions. Thus, his conceptual framework included the revolutionary notion of nature's inherent malleability, tacitly implying that species, by rule, modify when migrating to areas with differing habitats as a means to adapt to changing conditions (Buffon, 1761).

Nonetheless, Buffon stopped short of completely rejecting Linnaean theory despite the fact that he is often cast as Linnaeus' foil. Buffon wholeheartedly embraced the center of origin/dispersal model, concluding, as Linnaeus did, that the modern distribution of species is the

result of a single dispersal event from a primordial center of origin (Nelson & Platnick, 1981). However, a careful reading of Buffon's ideas reveals a potent inconsistency. On the one hand, he argues that distinct faunal assemblages in highly similar, but geographically isolated environments are the result of dispersal-induced morphological changes, but on the other he proclaims that morphological changes occur as species disperse to *novel* environments (Buffon, 1749, 1766). This inherent contradiction, of which Buffon was most likely aware, was the result of his reluctance to reject the single dispersal/primordial center of origin model championed by Linnaeus. Instead, Buffon simply replaced Eden with the vaguely defined "Old World" (Buffon, 1766; Linnaeus, 1781; Nelson & Platnick, 1981). By failing to reconcile his divergent ideas, Buffon cemented the notion of a single center of origin in the scientific community for decades to come.

Early 19$^{th}$ Century naturalist-explorers, such as Alexander von Humboldt (1816) and Pierre Latreille (1817), traveled the world seeking to corroborate Buffon's law. Humboldt and Latreille examined New World plants and insects respectively and worked within the Old World center of origin paradigm, essentially accepting that there existed a single world biota. However, as naturalists began to amass more observations from different corners of the globe, the mounting evidence began to suggest that an original dispersal from a single location might not adequately account for the wide variety of organisms that inhabit the earth.

In 1820, Augustin de Candolle published an essay titled *Géographique Botanique*, in which he proffered an alternate hypothesis for biogeographical distributions and biological variation. Candolle, though never having strayed far from France, cautiously studied the reports of naturalist-explorers like Humboldt and Latreille and began to question the scientific status quo (Nelson & Platnick, 1981). In his 1820 essay, Candolle not only discussed the external elements

that influence plants in measurable ways (temperature, light, water, soil, and atmosphere), he also explicitly differentiated between what he termed the "station" and "habitation" of any given species. These two concepts are now referred to as "habitat" and "geographical location" respectively and represent definitions crucial to the study of biogeography. In short, Candolle posited two discrete ways to investigate the reasons for any given species' biogeographical context. By examining a species' "station" (habitat) the naturalist seeks to understand the ways in which the external environmental elements affect its distribution, i.e. its *ecological* context. Alternately, by examining a species' "habitation" (geographical location) the naturalist seeks to understand the *historical* reasons for its current physical location on the earth. In Candolle's own words, "Stations are determined uniquely by physical causes actually in operation, and… habitations are probably determined in part by geological causes that no longer exist today" (1820:413).

What is most fascinating about Candolle's (1820) statement above is that he clearly proposes that the earth's geography might have been very different in the ancient past, tacitly suggesting that the distribution of species might be accounted for by yet to be described geological processes. In this simple conjecture, Candolle offers a resolution to Buffon's contradiction described above by presenting an alternate mechanism beyond dispersal by which species became distributed and differentiated across the globe (Morrone, 2009). In fact, Candolle (1820) went on to conclude that rather than a single center of origin for the world's species, there exist twenty-two biotic regions that represent discrete areas of endemism, each with its own independent natural history. Years afterward, Sclater (1858) refined Candolles's twenty-two

biogeographic areas into the six biotic regions that continue to be referenced today.[1] Candolle's (1820) ideas had profound significance to the nascent field of biogeography. By invoking geological processes, Candolle was the first to offer the framework for the concept of speciation through vicariance—the emergence of a physical barrier that separates a continuous population (Croizat, 1964; Nelson & Platnick, 1981). In 1853, Joseph Hooker came to just that conclusion in the introduction to *Flora Novae-Zelandiae*. While Hooker did not refer to "speciation" per se, he did explicitly present the idea that closely related taxa of geographically isolated regions in the Southern Hemisphere may have been "members of a once more extensive flora, which has been broken up by geological and climatic causes" (Hooker, 1853: xxxvi).

Thus, in the first century of biogeographical theory the two main mechanisms of biotic distribution were delineated: dispersal from an ancestral center of origin (or, "dispersalism") and vicariance. Simply put, dispersalism involves the crossing of barriers by species populations whereas vicariance involves the emergence of barriers dissecting populations (Platnick and Nelson, 1978). Both mechanisms result in more or less the same outcome: two isolated populations capable of evolving into two discrete species. The difference between the two merely lies in the timing—dispersal implies that the barrier is older than the divergent population, whereas vicariance implies that the population predates the barrier. During the 19$^{th}$ and early 20$^{th}$ centuries, vicariance had difficulty gaining traction due to the fact that scientific consensus favored the theory of permanentism, the idea that earth's geography was effectively

[1] Candolle's (1820) twenty-two biotic regions as subsets of Sclater's (1858) six ornithological regions: **1) Palaearctic** (Boreal Europe and Asia, Europe south of the Boreal region and north of the Mediterranean, Siberia, Mediterranean Sea, Eastern Europe to the Black and Caspian Seas, Japan); **2) Ethiopian** (South Africa, East Africa, Tropical West Africa, Canary Islands); **3) Indian** (India, China and Indochina**); 4) Australian** (Australia); **5) Nearctic** (Boreal America, Northern United States, Northeast coast of North America); **6) Neotropical** (The Antilles, Mexico, Tropical America, Chile, Southern Brazil and Argentina, Tierra del Fuego).

fixed in place. It was accepted that minor geological changes could occur, such as volcanic islands emerging from the sea, but the idea of entire *continents* shifting their positions was resoundingly rejected by most scientists (LeGrand, 1988). One particularly influential 19th century scientist who rejected the notion of geological/geographical instability (or, "mobilism") and effectively set the tone among biogeographers and natural historians for the next century was Charles Darwin (1859).

In Chapters 11 and 12 of *The Origin of Species* (1859), the biogeographical underpinnings of his theory of natural selection are made abundantly clear. Undoubtedly, Darwinian evolutionary theory is essentially incomplete without an understanding of biogeography—inter-group spatial distance and potential separation between populations allows for the variation upon which natural selection works. Yet, for Darwin, dispersal over physical barriers was deemed the primary method by which populations diverge and speciate. Darwin sided with the permanentists, likely due to his close association with Charles Lyell, whose three-volume masterpiece, *Principles of Geology* (1830-1833), laid out the theory of gradualism and described an earth, slowly eroding over long periods of time. Not surprisingly, Darwin's close ally and leading expert on biogeography, Alfred Russell Wallace, staunchly defended permanentism as well, though evidence from his own writings plainly demonstrates that he originally advocated the idea of continental movement as a means to explain species distributions (Camerini, 1993).

Nevertheless, Darwin explicitly stated in *Origin*, "I do not believe that it will ever be proved that within the recent period continents which are now quite separate, have been continuously, or almost continuously, united with each other…" (1859:358). Darwin thus formulated his opinions about biogeography without apprehending the validity of geological

instability and continental drift. At a deeper level, Darwin effectively kept the earth's geological processes disconnected from its biological processes. In this regard, many of his most ardent critics (e.g. Croizat: 1964; Croizat et al., 1974; Nelson and Platnick 1980,1981) contend that by favoring the center of origin/dispersal model, Darwin unconditionally rejected the possibility of vicariance. Darwin's own words seem to indicate otherwise:

> Hence it seems to me, as it has to many other naturalists, that the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is most probable… But the geographical and climatal [sic] changes, which have certainly occurred within recent geological times, *must have interrupted or rendered discontinuous the formerly continuous range of many species* (1859:353, emphasis mine).[2]

Clearly, Darwin wrestled with the possible mechanisms for species distribution, and several other passages from *Origin* clearly demonstrate the nuanced thinking that he applied to the subject. It bears mentioning that Darwin's rejection of nascent models of vicariance stemmed in part from his adamant repudiation of multiple centers of origin for life itself. Darwin strongly emphasized his tacit dismissal of creationism and his grand idea of common descent with modification: "Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the vera causa of ordinary generation with subsequent migration, and calls in the agency of a miracle" (Darwin 1859:352). What is more, it would appear that Darwin was frustrated with the fact that many of his contemporaries were apt to invoke extinct land bridges between areas now separated by sea seemingly without scientific rigor: "[A]uthors have thus hypothetically bridged over every ocean, and have united almost every island to some mainland" (Darwin, 1859:357). Be that as it may, Darwin essentially solidified the primacy of dispersalism in biogeography, and it was not

[2] Interestingly, Croizat, et al. (1974) utilize the same passage, conveniently omitting the final sentence.

until the 1960's and the eventual acceptance of Wegener's (1912, 1929) theory of plate tectonics that vicariance began to seriously resurface as a viable and vital mechanism by which species are distributed throughout the world (LeGrand, 1988).

This is not to say that the century after *Origin* was published, all scholarly work assuming a geologically dynamic earth ceased. Quite the contrary, trailblazing biogeographers continued to highlight the faunal evidence for land connections that no longer exist. Notably, Simpson (1940) pioneered theories regarding land bridges and mammalian distribution in North America and Madagascar. While he was staunchly opposed to the idea of continental drift, he nonetheless presented evidence that rejected the notion of outright geographical permanence, evidence that was most parsimoniously explained by extinct land connections (Schuh and Brow, 2009). Even during Darwin's lifetime, zoological evidence continued to suggest that dispersal throughout a geographically static earth could not adequately account for the observed floral and faunal distributions. In 1867, the zoologists Verrill and Günther pointed out that the marine life on either side of Central America bore intriguing similarities despite the fact that the Isthmus of Panama represented an insurmountable dispersal barrier between the two biotas (Ekman, 1953).[3] Years later, Ekman (1953) quantified the faunal similarities and demonstrated that the zoological evidence left no other conclusion: in the past, the two marine regions must have been connected as part of a single biota.

Despite the fact that modern geology confirms the hypotheses of Candolle (1820), Hooker (1853), and many others, the century during which notions of vicariance through

[3] In fact, in the sixth edition of *Origin of Species* (1872), Darwin comments on Günther's work in passing, noting that it seemingly contradicts his belief in the presence of distinct faunas on either sides of geographical barriers: "The marine inhabitants of the eastern and western shores of South America are very distinct, with extremely few shells, crustacea, or echinodermata in common; but Dr. Gunther [sic] has recently shown that about thirty percent of the fishes are the same on opposite sides of the isthmus [sic] of Panama" (p. 500-501).

geological activity were relegated to the periphery had a lasting effect. As a result of the historical feud between the staunch adherents of dispersalism and vicariance, the two conceptual approaches have often been cast in stark opposition to one another (Morrone, 2009). The debates are too numerous to recount here, suffice it to say that a patently false dichotomy has festered within biogeography for some time. At this juncture, ample evidence exists supporting both dispersal and vicariance explanations for species distribution. It seems as if reconciliation between the two will be most beneficial to our understanding of biogeographic patterns in nature, and in the last decade many researchers have reached a similar conclusion (Morrone, 2009; Parenti and Ebach, 2009).

In a tangential way, Candolle predicted the false dichotomy between the dispersal and vicariance models nearly 200 years ago. Candolle was acutely aware of the fact that his contemporaries often conflated the notions of station and habitation when investigating species dispersal, lamenting that "the confusion of these two classes of ideas is one of the causes that have most retarded the science and that have prevented it from acquiring exactitude" (1820:383). To reiterate, investigating a species' station requires an understanding of its ecological context whereas exploring the reasons for a species' habitation requires and understanding of its distributional history. The two concepts, though clearly related, require different scales of evidence just as, perhaps, dispersal and vicariance operate on two separate mechanistic scales. Notions of habitat quality and environmental conditions are particularly important when discussing speciation via dispersal, whereas vicariance models require an understanding of the geological and geographical history of the species distributional parameters. Could it be that the debate between the two approaches stems largely from a misunderstanding of their basic differences? Perhaps one approach is simply not applicable to every biogeographical question.

There is no question that the modern understanding of geology and plate tectonics fundamentally altered the way in which biogeographers view the world just as genetics revolutionized the understanding of biology. The modern era of biogeography was ushered in by the acceptance of continental drift, as well as by improvements in molecular biology and its contributions to the understanding of phylogenetic relationships between organisms. The last fifty years have seen the field of biogeography finally mature into the viable and comprehensive science it is today.

## Chapter 3: Biogeography Matures as a Discipline

### *Definitions:*

Before moving forward, a brief discussion of biogeographical terminology must occur. The major conceptual terms that must be adequately and concretely defined are: distribution, dispersal, dispersion, diffusion, migration, and area of endemism. Unfortunately, in much of the literature not specifically tethered to the study of biogeography, these terms are accorded multiple definitions. Particularly in the paleoanthropological literature, dispersal, distribution, and migration are often conflated. The definitions below represent those that are widely accepted in the biogeographical literature over the last ten years (Huggert, 2004; Morrone, 2009; Parenti and Ebach, 2009; Schuh and Brower, 2009).

The easiest definition to clarify is distribution. The distribution of an organism is quite simply the geographic area within which it is normally found—often referred to as its range. Distributions are not static and when quantified represent an assessment for a particular moment in time.

One of the biggest discrepancies comes when scientists speak about dispersal, dispersion, and diffusion. There is a nuanced relationship between the three as they all refer to the active movement of a species across the landscape. Speciation events can be fairly localized and it takes time for a new species to reach the limits of its distribution. Accordingly, no one would argue that the distribution of a taxon implies an instantaneous appearance across what will become its ancestral range. The term diffusion, though coolly received by scholars at first, is understood as referring to this initial movement of a population as it begins to spread throughout its distribution (Nelson and Platnick, 1981). It can also be used to refer to a population's coincident movement with the expansion of its native habitat. In other words, a species will diffuse to new geographic

areas as environmental conditions allow for the expansion of its native habitat into those areas as well.

Dispersion refers to the movement of an organism within its distribution and is not to be confused with dispersal. Dispersal is the movement of a taxon, often across a barrier, which results in the expansion of its distribution. Unlike diffusion, which is tethered to shifting habitats, dispersal implies that the agency of the organism alone is responsible for distributional expansion. Dispersal generally results in the occupation of novel habitats, a precursor to classic notions of allopatric speciation.

Perhaps the most widely abused term is migration. The confusion surrounding its biogeographical definition is likely the result of its common application to the geographical movements of modern human populations, not to mention the fact that Darwin (1859) used it synonymously with dispersal. Nevertheless, in modern biogeography (and all modern natural sciences for that matter) migration simply refers to the seasonal, regular movements of organisms within their accepted distributions—in essence, a particular and well-defined form of dispersion. It does not result in the occupation of novel habitats and is a behavior specific to certain migratory taxa. Migration is not synonymous with dispersal.

Endemism is similar to distribution, if not identical. A species is considered to be endemic to an area if it is found there and nowhere else. So-called “areas of endemism” are highly relevant to the study of biogeography and are defined as geographical locations containing the non-random distributional overlap of multiple taxa. Areas of endemism are understood to be the hallmarks of historical centers of species generation and taxonomic diversity.

There is no firm consensus on the terms above, and many are often slightly altered or augmented to suit particular authors' tastes (e.g. "geodispersal" (Lieberman, 2000)). Nonetheless, the somewhat conservative definitions above are quickly recognizable to anyone familiar with biogeographical research.

***Continents Adrift:***

As discussed in the previous chapter, an argument can be made that the Lyell-Darwin-Wallace support for permanentism stunted the growth of biogeography for roughly one hundred years (for discussion, see Parenti & Ebach, 2009). However, to attack these men's scientific judgment (see Croizat et al., 1974) is both misguided and counterproductive. No known geological mechanism supported Wegener's theory until Hess (1962) discovered the spreading mid-oceanic ridges that ultimately convinced the scientific community at large (LeGrand, 1988). If nothing else, Darwin and his cohort were taking a conservative approach in light of the available evidence and, due to their significant clout, convinced others to do the same. Yet, despite Darwin's tremendous influence on the subject, researchers continued to hypothesize about geology's role in species distribution even though they were at times working on the periphery of the mainstream (e.g. Newbigin, 1936; Simpson, 1940; Eckman, 1953; Croizat, 1958). Scientists continued to amass and describe the floral and faunal evidence for extinct geological features despite resistance from geologists themselves. These researchers' eventual scientific vindication clearly demonstrates that studies of the biotic world have much insight to offer the investigation of geological history. Whereas Darwin may have erroneously separated the earth's geological and biological histories, today the association between the two is rightfully

appreciated. In the modern era, geology and biogeography are finally working in tandem, adding to science's ability to make powerful and salient conclusions about the natural world.

Modern biogeography exists in a cross-disciplinary sphere not unlike many other contemporary sciences. Needless to say, with influence from multiple scientific traditions often come competing methodological interpretations, and biogeography has seen an explosion of theories in its recent history (see Morrone, 2009; Parenti and Ebach, 2009). Despite the tremendous time and energy that many biogeographers have spent supporting and attacking the various methodologies, it is neither relevant nor possible in this format to delve into the nuanced theoretical differences that have arisen between scholarly camps. When contemplating the multitude of readily identifiable, supposedly distinct biogeographical theories and approaches,[4] consensus holds that all can be broadly positioned into one of two general categories: *ecological* biogeography or *historical* biogeography (Morrone, 2009; Parenti and Ebach, 2009; Schuh and Brower, 2009). Much of the intra-disciplinary friction can be attributed to these two categorical distinctions, which are, in many ways, related to the established schism between dispersalism and vicariance models (Craw et al., 1999; Parenti and Ebach, 2009). Ecological biogeography has tended to favor dispersal as the mechanism explaining the biological patterns within its scope of research, whereas historical biogeography has tended to favor vicariance. While ecological and historical biogeography are often portrayed as being in opposition to one another (see Croizat et al., 1974) it is not difficult to discern that the two are intrinsically related and perhaps

[4] Morrone (2009:9) offers the following partial list of specialized sub-fields: regional biogeography, dispersalism, chorology, phylogenetic biogeography, paleobiogeography, panbiogeography, island biogeography, vicariance biogeography, Pleistocene refugia, dynamic biogeography, geographic ecology, areogeography, quantitative biogeography, cladistic biogeography, systematic biogeography, evolutionary biogeography, analytical biogeography, balanced biogeography, intraspecific phylogeography, macroecology, comparative phylogeography, applied biogeography, and the unified neutral theory of biodiversity and biogeography.

simply reflect differing scales of inquiry as previously suggested (Candolle's (1820) prescience was indeed remarkable).

In general, ecological biogeography concerns itself with species or population level distribution patterns that are dictated by biotic/abiotic interactions, and occur over relatively small temporal and spatial scales. At these small scales, dispersal events are simply more relevant to biogeographical interpretations. Island biogeography (MacArthur and Wilson, 1964) is perhaps the most well known example of the ecological approach. Island biogeography concerns itself with the ways in which species colonize and distribute within patches (islands) of suitable habitat that are surrounded by a non-habitat matrix—the pristine example being a terrestrial island surrounded by water. MacArthur and Wilson (1964) were able to estimate the distributions of taxonomic groups within patches provided they knew the size of the habitat and the distance it was from a "mainland" (original source of the taxa being studied). Clearly, island biogeography had great influence on the ecological community due to its relevance to conservation efforts concerned with how anthropogenic habitat fragmentation affects species populations. In fact, ecological biogeography is readily identified with the modern study of ecology and its emphasis on conservation and land management issues.

Historical biogeography tends to seek patterns at large spatial scales, and accounts for processes that typically happen over relatively lengthy periods of time, such as major geological transformation. Naturally, vicariance events become more evident when exploring the deep temporal history of biogeographical relationships. "Vicariance biogeography" (Croizat, 1974) is the quintessential example of the historical approach and simply holds that the patterns of modern species distribution can be fundamentally attributed to the disruption of taxonomic groups by abiotic forces such as geological and climatic change. Vicariance biogeography is

particularly insightful when looking at the distribution of flora across the globe, as demonstrated by Hooker's (1844-1860) interpretations of the plant species on Southern Hemisphere landmasses. Hooker recognized that the isolation of areas such as New Zealand, Australia, and Patagonia belied the fact that they share many families and genera of plants. As such, we now understand that these areas were part of the supercontinent, Gondwana, and that their current, seemingly enigmatic distribution is the result of continental fragmentation roughly 150 million years ago (LeGrand, 1988).

Many biogeographers (e.g. Crisci, 2001; Morrone, 2009) see ecological and historical biogeography as representing the extreme ends of what is essentially a continuum of methodologies. As with all continuums, the opposing endpoints are easily contrasted whereas distinctions get decidedly less clear as points of reference are positioned closer together. If we can agree that ecological and historical biogeography offer complementary avenues of inquiry just as dispersal and vicariance have both played a role in biogeographical distributions, we can conclude that differing approaches and theories must be applied on a case-by-case basis (Morrone, 2009). Clearly, ecological biogeographers require an understanding of the historical roots of modern biotic distributions just as historical biogeographers need to comprehend the ecological context of the taxa they are investigating.

For paleoanthropologists looking to understand the biogeography of hominins, an integrative approach akin to what has been coined "evolutionary biogeography" (Ridley, 1996; Morrone, 2009) offers the best toolkit of available methods.[5] Evolutionary biogeography calls upon elements of systematics, paleontology, geology, geography, ecology, and molecular

[5] There is seemingly little agreement as to the biogeographical method that bridges disparate theories most comprehensively. As such, depending on the author, any given "biogeography" can be deemed a sub-set of another.

biology as a means to forge its hypotheses and interpretations. As the name implies, varying temporal considerations are accounted for within its methodological parameters and different techniques can be applied according to need and applicability. In this regard, evolutionary biogeography does not treat vicariance and dispersal as conflicting explanatory models for the distribution of life. Instead, by examining the underlying biological patterns, it seeks to cogently incorporate species distribution, dispersal events, and vicariance within a valid ecological and temporal context (Morrone, 2009). For instance, evolutionary biogeography accepts that when environmental conditions are suitable, species will expand their distribution by diffusing across the landscape to the best of their capabilities, while also accepting the possibility of dispersal across barriers into novel habitats. Additionally, it is understood that vicariance events can and do occur within this context when the dynamics of the physical environment inevitably change over time. In general, the evolutionary biogeographical perspective can be viewed as a dispersal-vicariance model. It essentially confirms the concepts inherent to Darwinian dispersal and augments them with an understanding and appreciation of vicariance, thus accounting for the fact that the two generally happen at different scales (Morrone, 2009). More importantly, evolutionary biogeography allows for the paleobiogeographical interpretations required to understand patterns of hominin distribution. Thus, it offers specific methods that are appropriate for paleontologists in general, one of which is the utilization of Croizat's (1958, 1964) theory of "generalized tracks".

A discussion of modern biogeography would not be complete without looking to the work of Leon Croizat, the controversial figure who developed "panbiogeography", and whom some regard as a founding father of the modern era (Parenti & Ebach, 2009; Schuh and Brower, 2009). Croizat (1974, 1981) is perhaps best known for his unwavering attacks on Darwin and

particularly his rambling (some say incoherent) and unprofessional critiques of his theories (Schuh and Brower, 2009).[6] Pertinent to biogeography, Croizat continually assailed dispersalism and those who defended it, and insisted that vicariance offers the optimal explanation for the distribution of species on earth today (Parenti and Ebach, 2009). While his attacks may have been spurious at times, he validly challenged the stochasticity inherent to Darwinian dispersal models and presented evidence for loose patterns of distribution throughout the biosphere (Croizat, 1958). In his words, "Nature forever repeats" (Croizat, 1964, as cited in Schuh and Brower, 2009:212). Croizat (1958, 1964) viewed classic dispersalism as failing to explain what could be easily observed, and argued that far from being random, taxonomic distribution patterns remained relatively constant across regions and throughout time. He converted these distribution patterns into linear "tracks" that connected the "primary coordinates" of geographic distribution and were literally represented by lines drawn across a map. Most interestingly, Croizat's (1964) method was able to reveal trends of distributional (track) overlap between multiple, often highly variable taxa. These "generalized tracks" were informative because the taxa involved were phylogenetically distinct; therefore, their similar distribution was unlikely to have resulted from random dispersal. Thus, by examining multiple species, certain biogeographical patterns emerged.

For example, citing the work of Rosen (1974), Croizat noted that the wide intercontinental distribution of a group of freshwater fish (*Galaxiidae)* in the Southern Hemisphere could not be readily explained by chance dispersal from a center of origin, as would

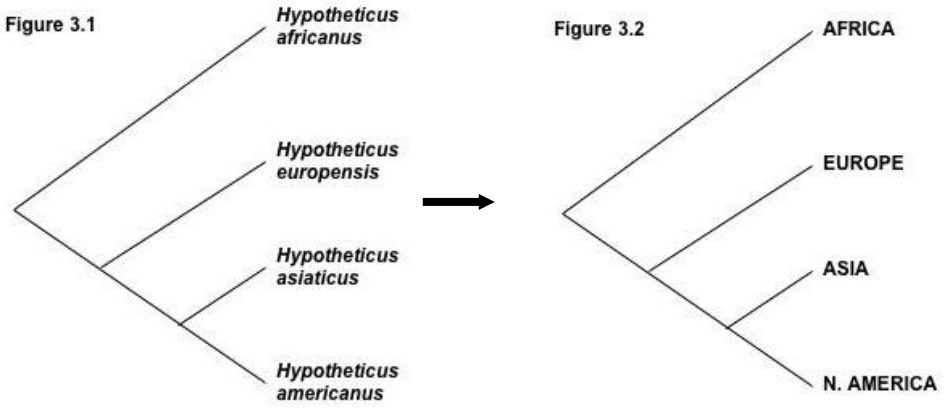
[6] For example, when discussing Darwin's biogeographical theories specifically presented in Chapter 12 of the sixth edition of *Origin* (1872), Croizat (1981) remarks: "The quality of Darwin's argument has serious implications; in my judgment it disqualifies Darwin as a theorist worthy of attention… he invites his peers to share, and to exhibit, ignorance as a badge of common wisdom" (p. 504).

be predicted by dispersalism alone. Instead, by broadening the scope of inquiry and accounting for the various organisms with similar distributions but different dispersal capabilities, a general track emerges that is shared by earthworms, crustaceans, mollusks, and birds, among others (Croizat, 1974). He concluded that the distributional similarities of such phylogenetically disparate organisms with different levels of vagility had to have been the result of vicariance events long ago that led to the fragmentation of multiple clades of austral organisms. In this regard, Croizat (1964) was working within the emerging geological paradigm that included plate tectonics, and noted that generalized tracks do not necessarily conform to the geographical markers of today. Croizat even suggested that the biotic and abiotic elements of environments are continually "coevolving", firmly conjoining biology with geology. When superimposing multiple generalized tracks, Croizat postulated that the nodes resulting from their intersections represented geographically consistent areas of endemism (Nelson and Platnick, 1981).

The idea of generalized tracks remains one of Croizat's (1964) most significant contributions to biogeography (Nelson and Platnick, 1981; Morrone, 2009). The idea that a species' distribution may be best understood by looking at multiple taxa with different phylogenetic backgrounds is certainly powerful, and gives the researcher a means to identify testable hypotheses regarding historical distribution patterns across regions (Nelson & Platnick, 1981). Nevertheless, the recognition of appropriate taxonomic units within these general tracks requires the adequate application of phylogenetic analysis. Scientists must be confident in their understanding of the interrelatedness of species and their position within broader taxonomic groupings. Thus, agreeing upon how a taxonomic group is adequately described becomes a necessity, and modern systematic analysis has helped biogeographers with just such a task.

Willi Hennig, the German systematist, had an undeniable influence on modern biogeography as well. Hennig (1960), the founding father of cladistics, introduced many biogeographical concepts into his work, including the "progression rule". The progression rule simply states that organisms will become more derived the further they are from their ancestral region of origin. That is, when trying to understand the phylogenetic and geographical relationships within a taxonomic group, more derived forms will be found at the peripheries of the ancestral distribution. This theoretical framework, dubbed phylogenetic biogeography, served as a template for all of his biogeographical and phylogenetic interpretations. Hennig worked against the backdrop of the emerging field of systematic biology that was dominated by the ideas of Ernst Mayr (1953) and George Gaylord Simpson (1961). Mayr et al. (1953) presented a neontological, microevolutionary view of biotic diversification in their seminal text, *Methods and Principles of Systematic Zoology*. However, their lack of attention to the deeper historical reasons for the classification of life bothered some, such as Simpson, a fossil mammal specialist. In *Principles of Animal Taxonomy* (1961), Simpson made the argument that species classification is incomplete without accounting for the temporal perspective provided by geology and the fossil record. Hennig synthesized the neontological and paleontological perspectives in order to not only understand, but also define the phylogentic and spatial relationships between organisms. Though the progression rule and phylogenetic biogeography are now widely discredited, Hennig (1966) conclusively established the need for a direct connection between phylogenetic analysis and the study of biogeography (Schuh and Brower, 2009). Crucially, phylogenetic biogeography served as the foundation for the cladistic analyses that are widely used today by historical biogeographers and are most pertinent to research utilizing the fossil record (Morrone and Crisci, 1995).

Gareth Nelson, Norman Platnick (1981), and Don Eric Rosen (1981) built upon the ideas of Hennig and began manipulating the cladistic analyses that were central to his approach. Hennig developed cladistics as a means to classify organisms into monophyletic groups (clades). His visual depictions of these groups, cladograms (Fig. 3.1), lead Nelson and Platnick (1981) to proffer the notion that common biological ancestry in turn implies common geographical ancestry. Based on the premise that the phylogenetic and geographical area relationships among taxa correspond in ways that are biogeographically informative, Nelson and Platnick (1981) developed the method for constructing "area cladograms" (Fig. 3.2). This technique became the core feature of what is now defined as cladistic biogeography. The construction of area cladograms is straightforward, and simply entails the translation of the traditional, biological cladogram into its spatial equivalent. At the terminal ends of the cladogram tree, the named taxa are replaced by the geographical area(s) in which they are distributed (Fig. 3.1; Fig 3.2). The result is a model of the "phylogenetic" relationships between the geographical areas being studied (Nelson and Platnick, 1981).




**Figures 3.1 and 3.2.** In this scenario, four members of a hypothetical genus are presented in a cladogram depicting their phylogenetic relationships (Fig. 3.1). In order to construct the relevant area cladogram, their species names are replaced by their distributions implying the "phylogenetic" relationships of the corresponding geographical areas (Fig. 3.2).

Based on area cladograms, interpretations can be made regarding the biogeographical histories and connections between clades of organisms and their relevant geographical areas. In other words, the intertwined history of a taxon's spatial genealogy can be clarified. The proper manner in which to interpret area cladograms has been a source of contention among historical biogeographers ever since (Morrone and Crisci, 1995; Morrone, 2009; Parenti and Ebach, 2009; Schuh and Brower, 2009). There are clear limitations to the construction of area cladograms, the most obvious of which are the reliance on adequate phylogenetic interpretations, an adequate understanding of the distributional parameters of the taxa being investigated, and a legitimate division of landscapes into defined areas for analysis (these potential deficiencies are discussed in Chapter Five). Nonetheless, several researchers over the years have offered their designs for the proper way in which to analyze a completed area cladogram in order to obtain the relevant biogeographical information.

The first hurdle that had to be overcome was the interpretation of area cladograms that are based on geographically widespread taxa. Widespread taxa pose a problem because they often result in area cladograms with terminal ends containing repeated geographical areas. This potentially confounds biogeographical interpretation because it implies a reticulated evolutionary history for the taxa being investigated (Folinsbee et al., 2007). In theory, vicariance events should be fairly clear from the examination of area cladograms due to the fact that, by definition, they result in discrete distributions between sister taxa. In practice, the widespread organisms that are generally encountered during actual field research are potentially the result of vicariance events intermixed with episodes of dispersal and possibly episodes of reticulated evolution. Scenarios such as these have the effect of clouding biogeographical interpretations (Morrone and Crisci, 1995). This evidence of reticulation requires a means by which to disentangle and

interpret the biogeographical information, and Nelson and Platnick (1981) devised a method in which area cladograms could be adequately resolved.

In brief, a "resolved area cladogram" based on widespread reticulated taxa incorporates the application of "assumption 0", "assumption 1", and/ or "assumption 2" (Nelson and Platnick, 1981). Assumption 0 considers area cladograms as being based on a monophyletic taxonomic group. Assumption 1 considers the area cladograms to be based on a monophyletic *or* paraphyletic group, and assumption 2 considers it to be based on a monophyletic, paraphyletic, *or* polyphyletic group (Morrone, 2009). Examining an area cladogram with theses assumptions in mind, interpretations can be made regarding the appropriate biogeographical mechanisms to infer. Needless to say, there is the potential for the *ad hoc* application of each of the assumptions above, and without going into detail, this fact has been a wellspring of criticism over the years. Also, by definition, cladograms depict monophyletic groups. Agreeing to assume that they can be translated into representations of para- or polyphyletic relationships is at the very least problematic. Thankfully, Nelson and Platnick's (1981) methods have been refined and improved over the years so a discussion of the application of assumptions 0, 1, and 2 is both unwarranted and unnecessary. Suffice it say, Nelson and Platnick (1981) established cladistic biogeography as a viable and insightful avenue of investigation for research and their contributions to the field cannot be overstated.

One of the most significant improvements to the methods listed above was the development and implementation of parsimony analysis to cladistic biogeography. Several forms of parsimony analysis have emerged over the years, but all can be more or less understood with regard to the widely used "Brooks parsimony analysis" (BPA) (Brooks et al., 1981). BPA is a method by which biogeographical information can be gleaned from the ancestral nodes that

characterize a cladogram tree. By assigning a biogeographic state to each of these nodes based on the areas being investigated, a data matrix noting the presence or absence of each geographic area at each terminal end *and* ancestral node can be generated (Lieberman, 2002) (Fig 3.3; Table 3.1)

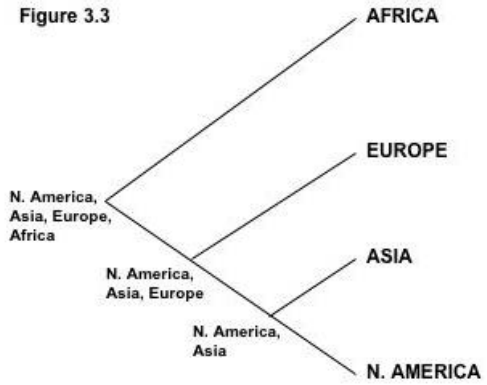



**Figure 3.3.** Based on the area cladogram in Fig. 3.2, the ancestral nodes are given geographic values in order to conduct parsimony analysis. In this scenario, the assumption is made that each ancestral node is represented by the inclusion of all descendent geographical areas. This technique rarely applies and is only depicted for its simplicity. Instead, algorithms are applied that affect the biogeographical values for each ancestral node.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Africa | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| Europe | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| Asia | 1 | 0 | 1 | 0 | 1 | 1 | 0 |
| N. America | 1 | 0 | 1 | 0 | 1 | 0 | 1 |

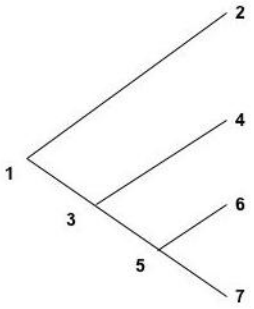



**Table 3.1.** Above is the coding table for the area cladogram depicted in Fig. 3.3. The geographical areas are represented by the rows, and the nodes and terminal ends are represented by the numbered columns (the numbering system starts from the ancestral stem of the cladogram and works its way up the tree as depicted on the right). Absence of an area from a node or terminal end is depicted by a "0" and presence is depicted by a "1". For analytical software, an "ancestor" row of all zeros must be added.

By applying specific algorithms, such as the Fitch algorithm (Fitch, 1971) (Appendix 1), the geographic states of the ancestral nodes can be organized in a way that provides specific biogeographical interpretations concerning events of dispersal and vicariance. In essence, these

algorithms "edit" the biogeographical character states, enabling the area cladogram to depict incidents of distributional expansion and contraction between sequential ancestral and descendant nodes. Expansion of distribution is then interpreted as evidence of dispersal whereas contraction of distribution is considered evidence of vicariance. In the corresponding data matrix, a "2" is placed in the cell that corresponds with either a dispersal or vicariance event, depending on the analysis. As such, area cladograms generate a separate "dispersal" and "vicariance" data matrix in order to identify the two (see Chapter Five for a detailed example).

One of the newer methods that has been applied to paleoanthropological investigations (Folinsbee, 2009; Folinsbee and Brooks, 2007) is PACT (phylogenetic analysis for comparing trees) (Wojcicki and Brooks, 2005). PACT is essentially a version of BPA, differing only in its use of a unique algorithmic manipulation of area cladogram data (see Wojcicki and Brooks, 2005). As can be seen, modern cladistic biogeographical methods are well suited to the researcher seeking to gain biogeographical information from the fossil record. However, the majority of biogeographers have not always supported the use of cladistic analysis for paleobiogeographical interpretations (Lieberman, 2002; Upchurch et al., 2002). A brief discussion of the trepidation inspired by the use of the fossil record is warranted.

While the fossil record is notoriously incomplete, it nonetheless samples a wide variety of organisms in specific locations across time. Even with sparsely represented specimens, the presence of multiple species at fossil sites implies that scientists can potentially infer biogeographical relationships across regions and theoretically, across time spans. Yet, biogeographers have traditionally been reluctant to quantify ancient distribution patterns based on the fossil record for several reasons, namely that the presence of a fossil taxon at a particular site is in no way equivalent to its absence. Whereas an organism's fossil presence at a site

indicates that it was indeed inhabiting the study area at the time period being sampled, its absence could mean one of three things: 1) it did not exist there (genuine absence); 2) it lived there at one time but became extinct (regional extinction); or 3) it lived there, but for whatever reason evidence was not preserved in the fossil record or has not yet been found (pseudo-absence) (Lieberman, 2000; Upchurch and Hunn, 2002, Upchurch, et al., 2002). Traditional attempts at paleobiogeography have mostly ignored this discrepancy and have thus been discounted by many scientists. Paleobiogeographers have often utilized what are essentially hypothetical narratives based on dispersalist interpretations that value "absence" in the fossil record as legitimate data (Lieberman, 2000). In turn, by giving equal weight to presence and absence data, paleobiogeographers have traditionally utilized temporal data to give "polarity" to their narratives despite the potential for gross misinterpretations (Fig. 3.4) (Upchurch and Hunn, 2002).

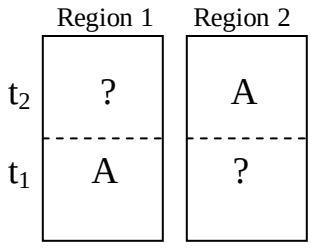



**Fig 3.4.** Two separate but neighboring geographical regions, each divided into two sequential time periods ($t_1$ and $t_2$) containing fossil evidence for Taxon A. The literal interpretation that gives equal weight to the presence *and* absence of data will interpret Taxon A as having dispersed/diffused from Region 1 into Region 2 after which it went extinct in Region 1. However, the missing data (the question marks) do not prove the absence of Taxon A from those regions or time periods and do not indicate polarity.

Over the last decade, paleobiogeographers have begun to shift away from the narrative approach and attempt to formulate quantifiable and testable hypotheses based on the fossil record. Upchurch et al. (2002) pioneered a new method while attempting to tease out the signals of vicariance and dispersal events experienced by dinosaurs. By dividing their data into "time

slices" and utilizing only the presence of taxa across sites, Upchurch et al. (2002) sought to remove the ambiguities of the narrative approach while still accounting for the importance of the temporal information preserved in the fossil record. In fact, they rightfully note that cladograms effectively remove time from analyses when, as is often the case, temporally fragmented taxa are depicted on the same tree. After culling global fossil data from nine different time periods ("slices"), they used TreeMap software (Page 1994, 1995) to generate an "optimal area cladogram" for each utilizing recognized phylogenetic relationships among 152 different taxonomic groups. By sampling across a wide spectrum of species, Upchurch et al. (2002) hoped to demonstrate that non-random, overlapping area relationships would emerge that identified regional vicariance events indicating generalized dinosaur distributional tracks. Because of their reliance on presence data alone, the ability to discern significant patterns of dispersal and vicariance within each time slice was diminished. However, by "vertically" comparing multiple time slices with the use of TreeMap software, non-random ($p < 0.05$) patterns of vicariance emerged for three of their nine time slices. Citing the particular inadequacies of the dinosaurian fossil record, Upchurch et al. (2001) nonetheless demonstrated that biogeographical patterns can be statistically and analytically tested based on fossil evidence. In light of the patchiness of the dinosaurian fossil record, other paleontological inquiries may potentially fare better. Clearly, this new technique has profound implications for paleoanthropologists seeking to understand the biogeography of early hominins. However, consideration must be given to the fact that the temporal scale of the study above was such that each time slice spanned roughly 25 million years. Nevertheless, the method does not seem to preclude its application to more fine scale interpretations.

In light of the current trends in biogeography, it may be time for paleoanthropologists to reassess past attempts to reconstruct the history of hominin distribution patterns. While evolutionary biogeography ultimately offers the best model for interpreting the past distributions of extinct organisms, there nonetheless remain key problems specific to hominin biogeography that must be addressed. As alluded to, the major hurdles in investigating any long extinct community include the irregularities of the fossil record and the formulation of competent taxonomies. The latter is particularly treacherous in the field of paleoanthropology (see Tattersall, 2009). Paleobiogeographers account for the inherent weaknesses of the fossil record in their methods, but taxonomic assessments represent a true limiting factor in accuracy of one's results. A case can be made that arguments within paleoanthropology concerning appropriate hominin taxonomic definitions are particularly contentious, and that hominin genealogy is essentially unresolved (Klein, 1999; Tattersall, 2009). An agreed upon hominin phylogenetic assessment becomes imperative for scientists looking to apply biogeographical methods to paleoanthropology. Nonetheless, the major ingredients for a modern biogeographical study of hominins are certainly attainable.

Most, if not all, biogeographical studies within paleoanthropology have looked to one group of mammals (e.g. bovids, carnivores, rodents) in isolation rather than choosing disparate groups of organisms (see Grubb et al., 1999; Strait and Wood, 1999; Fleagle and Gilbert, 2006; Turner and O'Regan, 2007). In order to adequately understand hominin distribution, paleoanthropologists must contextualize our ancestors within their broader ecological settings by examining a range of associated organisms with which they shared the landscape. Also, it may be time for paleoanthropologists to distance themselves from the narrative approach as described earlier. Evolutionary biogeographers explicitly refute the notion that the ancestral area of

endemism of any given species is necessarily represented by the location where the oldest fossil representative has been discovered (Morrone, 2009). While this may seem patently obvious, if one examines some accepted hypotheses regarding hominin distribution they generally "start" in East Africa. In fact, the East-South hominin dichotomy may or may not be drastically misrepresented and misunderstood. Without rigorous analytical studies, paleoanthropologists are left with little more than the polarized, "just so" stories that are being questioned by today's paleobiogeographers. These narratives are no doubt good for generating hypotheses, but they do not have the ability to be scientifically tested themselves (Popper,1959, 1963; Upchurch et al., 2002).

What is more, by broadening the range of organisms utilized in paleoanthropological research, new avenues of discovery are likely to open. For example, paleoanthropologists have been apt to ignore the Zambezian region of Africa situated between the East and South African hominin sites (but see Bromage and Schrenk, 1995; Bromage et al., 1995). This area undoubtedly contains crucial information that is central to hominin evolutionary history but has been overlooked in the past due to the paucity of hominin remains that have been recovered there (Kingdon, 1989, 2003). It seems evident now that a lack of hominin fossils does not theoretically preclude the region's inclusion in biogeographical analysis provided other appropriate taxonomic groups have a fossil history in the area. The simple geographic location of the region in relation to what is currently known about hominin distribution patterns demonstrates that the Zambezian region represents a gaping hole in paleoanthropological research. Its common characterization as a "corridor" (see Strait and Wood, 1999) between East and South can no longer suffice. While biogeographical interpretations related to the hominin fossil record have been explicitly

proffered (e.g. Strait and Wood, 1999), it can be argued that more work needs to be done in order to exhaustively flesh out all potential interpretations.

## Chapter 4: Past Paleoanthropological Applications

As one would expect, physical anthropologists have incorporated biogeographical interpretations into their scope of research for decades. However, because of biogeography's multiple manifestations, the degree to which anthropologists apply biogeographical methods and theories varies greatly. Many authors begin and end their inquiries by simply relating the temporal presence and/or absence of taxa across regions, much as you might find in a naturalist's field guide. Others may follow their descriptions of distributional patterns with narratives regarding the possible mechanics behind them, basing their hypotheses on a wide variety of evidence (e.g. ecological parameters, climate, geology, etc.). Still others may take a step further and demonstrably compare the distribution of multiple taxonomic groups across regions through time. Clearly, each of these levels of inquiry represents a form of biogeographical discussion, ranging from analysis of the readily apparent, *prima facie* evidence to more in-depth investigations.

This variability requires that those seeking to glean pertinent biogeographical interpretations from previous studies must precisely understand the scope and scale not only of their own research, but also of the work being examined. If we are going to attempt to approach testable, cladistic biogeographical interpretations of hominin evolution we must build off of the literature containing usable data and hypotheses suitable for further study. Fortunately, the data collecting groundwork for modern biogeographical interpretations within paleoanthropology has been laid. Unfortunately, the field is also clouded with ostensibly biogeographic studies that bear little resemblance to the testable analyses being sought. For example, a recent article (Morwood and Jungers, 2009) concerning the discovery of *Homo floresiensis* features the word "biogeography" prominently in its title. However, the actual biogeographical discussion within

the paper consists of little more than the recognition that *H. floresiensis* expands the diversity and geographic range of hominins. Adhering to the narrative paleobiogeographical approach discussed earlier, Morwood and Jungers (2009) proceed to postulate that 880 Ka, a tsunami may have rafted a founding hominin population to the island of Flores. It is by no means my intention to disparage Morwood and Jungers, nor do I have any desire to disturb the hornets' nest that is the endless controversy surrounding *H. floresiensis*. The simple point to be made is that paleoanthropology may rightfully be accused of not always taking a rigorous and contemporary approach to biogeography despite explicit claims to the contrary. Nonetheless, many serious biogeographical studies have been undertaken with specific regard to hominin evolution. Although most researchers have yet to apply some of the more recent cladistic-based biogeographical methods, the data collected and organized over the past three decades clearly provides adequate foundation for future study.

As noted, understanding the legitimate biogeographical context of any given taxon requires a comprehensive examination of its spatial and temporal relationship with other organisms on the landscape (Croizat, 1964; Nelson and Platnick, 1981; Lieberman, 2000; Morrone, 2009). This is particularly crucial for paleoanthropologists for the practical reason that hominin remains are relatively rare when compared to other taxonomic groups found in the fossil record (White, 2005; Tattersall. 2009). That being said, there is a deep history of cataloging the associated non-hominin remains found at hominin fossil sites, albeit for reasons often unrelated to biogeography.

Associated faunal remains have long served as primary indicators for the paleoenvironmental conditions faced by extinct hominins, and extrapolating the ecological context in which hominins evolved has remained one of the major research goals of

paleoanthropologists since the earliest days of the discipline. For example, Raymond Dart's (1957) (in)famous hypothesis endowing australopiths with an "osteodontokeratic culture" represents a particularly florid interpretation of the faunal taxa found in association with hominin fossils. While decidedly misguided and incorrect, Dart nonetheless based his ideas on the broad physical evidence at hand in order to contextualize the ecological landscape within which hominins lived—a prime example of anthropology's early attempts to move beyond simple description and classification and into the science of interpretation (*sensu* Washburn, 1951). Non-hominin fossils continue to provide insight into the ecological parameters of our evolutionary past. Beyond their ecological implications, diverse groups of fossil taxa also lend clues into the patterning and oscillations of hominin distribution relative to their biotic counterparts. In a very real way, these extensive fossil data represent the necessary core ingredients for future paleobiogeographical research that seeks to utilize the latest methods. A few of the biogeographical studies from the paleoanthropological literature that will prove valuable moving forward are described below.

Elisabeth Vrba (1980, 1985, 1992, 1993) deserves much credit for pioneering a dedicated biogeographical approach to paleoanthropology (Lieberman, 2000). Vrba is most widely known for her "turnover pulse hypothesis" (1985, 1993), which places hominin evolution in a discretely biogeographical context based on her careful study of the evolutionary trajectories of African bovids over the last five million years. The turnover pulse hypothesis predicts that the drastic climatic shifts that occurred periodically in the past caused congruent speciation and radiation events ("pulses") among a wide variety of taxa and are perhaps indicative of the abiotic mechanisms responsible for the seemingly correlated speciation events suggested by the hominin fossil record (Vrba, 1992). As early as 1980, Vrba began exploring the potential application of

the “cladistic revolution” (Hennig, 1966) to the interpretation of African biotic history, recognizing that as molecular biology began to provide greater insight into the phylogenetic relationships between organisms so increased the resolution of macroevolutionary events in the evolutionary past. Vrba (1985, 1992) sought to uncover quantifiable evidence among the improved phylogenetic interpretations as a means to understand the habitat dynamics and resulting speciation events that they expose. Her work with bovids and attempts to correlate bovid and hominin speciation pulses with the available climatic and geological data remain strong examples of an authentic biogeographical approach—the correlation of earth’s biotic history with its abiotic past. Vrba (1980, 1985) was very much influenced by the theory of punctuated equilibrium (Eldredge and Gould, 1972) and saw support for its underlying assumptions in the apparent bursts of adaptive radiation in Plio-Pleistocene African fauna. Needless to say, Vrba (1985, 1992, 1993) compiled an abundant set of data regarding the fossil history of African bovids, which on its own represents a monumental contribution to paleoanthropology.

Whereas Vrba focused on bovids, others have turned to alternate clades of mammals for biogeographical interpretations of hominin evolution. Micromammals have been investigated by Wesselman (1995), Avery (1988, 1995), Denys (1999), and Reed (2005) to name a few. These authors primarily sought to extrapolate the vacillating, localized ecological conditions of the past based on the micromammal fossils recovered from multiple African sites. In doing so, their research necessarily focused on the distribution of species through time under the prevailing assumption that taxonomic distributions will tend to track with changing environments (for discussion, see Hopley et al., 2006; Campbell et al., 2011).

Denys (1999) applied statistical analyses to the presence and absence data for Plio-Pleistocene micromammalian taxa across eastern and southern Africa. She analyzed temporal patterns of species richness and relative abundance across regions in order to reconstruct the biotic flux that potentially influenced hominin distribution. Denys (1999) based her research on the premise that hominins may have strictly adhered to specific environments just as is presumed for many of the micromammals being studied, and her results indicated that there were past faunal connections between eastern and southern Africa. Denys (1999) looked for East-South continuity across three distinct time periods, the Early to Middle Pliocene (5 – 2.5 my), the Late Pliocene to Early Pleistocene (2.5 – 1 my), and the Middle to Late Pleistocene (1 – 0 my).[7] Evidence emerged that biotic components alternately shifted both northward and southward across the eastern half of sub-Saharan Africa during key periods of hominin evolution. Similarly, Avery (1988) utilized ecological methods such as the Shannon diversity index (Shannon, 1948) in order to uncover non-random patterns of past biogeographic distributions. Additionally, authors such as Reed (2005) have demonstrated that owl-accumulated micromammal fossils, such as those typically found at hominin cave sites, are particularly reliable representations of true species presence and abundance, further legitimizing the use of micromammalian evidence in biogeographical research. Needless to say, authors such as those above have amassed and organized sizable data sets that can be plugged into future cladistic analyses looking for specific biogeographical interpretations.

Other faunal groups that have been examined in a similar manner are carnivores (Werdelin and Lewis, 2005), primates (Benefit, 1999; Fleagle and Gilbert, 2006; Turner and

[7] The International Commission on Stratigraphy (ICS) has recently redefined the base of the Quaternary and pushed back the date of the Pliocene-Pleistocene transition to 2.6 million years before present (http://www.stratigraphy.org).

O'Regan, 2007), suids (White, 1995) and a wide range of ungulates and other large mammals (Klein, 1894; Bromage et al., 1995; Grubb et al., 1999; Bobe et al., 2001). Each study has varied slightly in its approach to biogeographical description but inevitably has based its conclusions on literal readings of the fossil record. Undoubtedly, all of the studies noted thus far have been insightful and important in furthering our knowledge regarding the ecological context in which ancient hominins lived and have contributed significantly to the overall accumulations of data that may serve as the basis for future research. While most of these studies focus their research on the non-hominin taxa and relate their results to hominin evolutionary history in the concluding pages, some paleoanthropologists have precisely included the hominin clade in their methods and analyses.

Turner and Wood (1993) attempted one of the first temporally precise, hominin-specific biogeographical studies in paleoanthropology with their attempt to reconstruct the phylogenetic relationships of the paranthropines. Whereas paleoanthropology had long relied on morphological description and analysis as a means to infer phylogenetic relationships between hominin taxa, Turner and Wood's (1993) implementation of a biogeographical approach was certainly groundbreaking. What is more, they applied biogeographical methods to a specific issue being debated among paleoanthropologists—the potential paraphyly or monophyly of *Paranthropus*. Turner and Wood (1993) examined the large mammalian African fossil record in eastern and southern Africa, including hominins, from the last four million years and applied Simpson's (1960) Faunal Resemblance Index (FRI) in order to discern the temporal patterns of distribution within, between, and across the two regions. The FRI values produced indicated periods of faunal overlap between the east and the south that implied the dispersal of varied taxonomic groups both northward and southward. Based on the temporal relationships between

the paranthropine species, they concluded that a monophyletic paranthropine genealogy is most congruent with the general biogeographical trends. They support an evolutionary scenario in which *Paranthropus aethiopicus* emerged in East Africa, later giving rise to *P. boisei* in the east and *P. robustus* in the south.

As a direct sequel to the study above, Strait and Wood (1999) furthered the analysis by applying the methods of cladistic biogeography. In doing so, Strait and Wood (1999) were the first paleoanthropologists to employ cladograms in an investigation of hominin biogeographical history. They examined the spatial relationships among hominin species and compared them to the faunal distributional data compiled by Turner and Wood (1993) in an attempt to correlate hominin biogeographical history with the broad biogeographical trends of the past. They rightfully acknowledged that no single agreed-upon hominin phylogeny exists among researchers, and therefore they applied multiple iterations of the hominin cladogram to their analyses. Interestingly, despite noting their application of cladistic biogeography, the authors stopped short of utilizing area cladograms in their analysis.

> [T]he formal methods of cladistic biogeography, in which biogeographic patterns are tested by examining area cladograms, cannot be applied here because data are available from too few regions. Cladistic biogeography requires faunal information from at least three areas[8], and although three regions are defined here, only eastern and southern Africa have been well sampled. Faunal representation from the Corridor is limited (Strait and Wood, 1999:9197).

Strait and Wood (1999) have an argument—a dearth of data is not conducive to sound cladistic analysis. However, instead of constructing area cladograms, Strait and Wood (1999) developed "phyletic trees" depicting the biogeographic genealogy of the hominins, which are

[8] Though a nuanced point, it is important to note that Nelson and Platnick (1981) (whom Strait and Wood (1999) cite) simply argue that the use of two regions is unlikely to produce results of significant value.

strikingly similar to the interpretations they claimed to be precluded from making. As they themselves note, "Biogeographic patterns were reconstructed by using parsimony to identify the regions occupied by the hypothetical ancestors located at the internal nodes of the cladograms and phyletic trees" (Strait and Wood, 1999:9197). Also, three regions were in fact used in their phyletic tree analysis. Granted, the data from the "Corridor" may be poor, but its inclusion in traditional cladistic biogeographical analysis is not forbidden by any means. Not to mention, Bromage et al. (1995) conducted research in the Malawi region in order to specifically obtain biogeographical data—relevant evidence is available (also see discussion in Bromage and Schrenk, 1995). Unfortunately, much of Strait and Wood's reluctance to use the "Corridor" as a legitimate third region may have stemmed from their preconceived notions about its biogeographical importance. "[T]he Corridor is likely to have served as a faunal conduit between the two other regions [eastern and southern Africa]" (Strait and Wood, 1999:9196). In other words, Strait and Wood were firmly committed to a narrative, dispersalist interpretation of hominin biogeography and were trying to flesh out the polarity of the dispersal events of the past. The fact that hominins may have been endemic to the "Corridor" is lightly considered.

As such, Strait and Wood (1999) offer multiple interpretations of possible hominin dispersal patterns between eastern and southern Africa based on their use of multiple hominin cladograms—claiming each set of results to be valid in its own context. The authors correctly note that phylogenetic interpretations of the hominin clade have a fundamental impact on biogeographic interpretations and therein lie the true grounds for debate. While they do not side with one hominin biogeographical pattern or the other, they come to the thought provoking conclusion that "hominid dispersals between eastern and southern Africa appear to have been more frequent than previously thought, and some of those dispersals may have opposed

prevailing mammalian trends" (Strait and Wood, 1999:9199-9200). Unfortunately, one potential flaw in their analytical technique is apparent. Although they apply cladistic analysis to the hominin record, they compare their findings to faunal interpretations based on FRI analysis (Turner and Wood, 1993), as noted above. A comprehensive cladistic biogeographical study would need to incorporate cladistic analysis of the faunal data as well.

Nonetheless, Strait and Wood (1999) demonstrated that cladistic analysis reveals a periodic faunal connection between the eastern and southern regions of Africa, similar to the ecological previously mentioned. Though Strait and Wood (1999) reified the East-South narrative dichotomy, because of their use of cladistic analysis, their work remains a significant benchmark in the study of hominin biogeography. Later research expanded on this theme as will be discussed below.

In more recent years, researchers such as Folinsbee (2009) and Folinsbee and Brooks (2007) have utilized more refined analytical techniques to uncover the biogeographical patterns of hominins and their hominoid ancestors. Notably, these authors moved away from the preconceived, dispersal-based interpretations outlined above noting that modern cladistic analyses can potentially tease out both dispersal and vicariance events from the fossil record (Lieberman, 2000, 2003a, 2003b). In this regard alone, these studies represent a leap forward in biogeographical analysis pertaining to paleoanthropological research.

Folinsbee and Brooks (2007) employed the PACT method as a means to synthesize the area cladograms of hominoids, hyaenids, and proboscidians during the Miocene. To reiterate, PACT is essentially a variant of BPA in that it seeks to find a parsimonious congruence between the biogeographical histories of two or more clades with the intent of discovering non-random overlapping patterns. Their results yielded biogeographical relationships within these taxa that

imply both broad evolutionary congruence and clade-specific dispersal and vicariance events, most notably hominin "evolutionary acceleration" over the past 5 million years (Folinsbee and Brooks, 2007).

PACT was also employed by Folinsbee (2009) in her investigation of the Papionin monkeys and their potential relevance to hominin evolutionary history. By testing the area relationships between bovid, shrew, squirrel, hippo, hominoid, and baboon phylogenies, Folinsbee (2009) sought to empirically test multiple hypotheses regarding the climatic and tectonic driven nature of the Neogene mammalian speciation patterns in Africa. Her results also demonstrated that both dispersal and vicariance signals can be detected in the fossil record and that PACT is capable of identifying specific zones in which speciation and dispersal events occur at a clade-specific level. Most notably, unlike Strait and Wood (1999), Folinsbee (2009) compared hominin specific cladistic analysis to cladistic faunal analyses, performing the morphological analysis on the papionin clade herself in order to fully develop their phylogenetic relationships.

There is no arguing that the use of modern biogeographical methods in paleoanthropology has progressed over the last decade. However, an argument can be made that the full potential of biogeographic analysis has not be reached. Unfortunately, many of the past biogeographical studies such as those described above stand in isolation from one another. Researchers often attempt to portray their particular choice of taxonomic group(s) as representing the best possible proxy for hominin reconstructions. These arguments are understandably based on the potential ecological correspondence between hominins and any given taxonomic proxy (Reed, 1997). For example, those studying large mammals (e.g. Turner and Wood, 1995; Strait and Wood, 1999) contend that hominins, being large mammals

themselves, can only be understood in reference to other similarly sized organisms. Alternately, scientists studying micromammals (e.g. Denys, 1995; Reed 2005) contend that hominins did not range across landscapes like migratory ungulates and are best modeled after species with close affinities to discrete habitats. Naturally, those examining the biogeography of African primates (e.g. Dunbar, 1983; Jolly, 2001; Folinsbee, 2009) point to their shared phylogenetic history with hominins as concrete proof of their relevance to hominin biogeography. In essence, an argument can be made to support the use of any given taxon based on a variety of assumptions. This does not mean that legitimate differences do not exist regarding the applicability of one taxon or another. Simply put, rather than standing in isolation, there needs to be integration of the available research as a means to forge ahead with innovative biogeographical interpretation. Developing a manner in which to accomplish this feat will be a demanding project for those willing to make the attempt.

The divisions and isolation between research parameters noted above may be decidedly contrary to a comprehensive biogeographical approach (Andrews, 2007). Because of the variability in methods and analytical applications, integrating studies such as those above may be problematic. For now, applying some of the basic cladistic analyses to all of the data on diverse taxonomic groups is both achievable and warranted. Though seemingly straightforward, this goal represents a Herculean task. Many of the necessary phylogenetic interpretations potentially do not exist and access to unpublished faunal data may require tremendous effort to obtain. Also, with specific regard to hominin biogeography, the paucity of data from the Zambezian region, as noted by Strait and Wood (1999), is highly problematic. Gathering these data could very well be beyond current possibility for a host of reasons, though the work of Bromage and Schrenk (1995) and Bromage et al. (1995) demonstrates that it can be done. In fact, the Hominid Corridor

Research Project began studying the Malawi region in 1983 and collected data on the ecological, geological, and paleoanthropological history of the region (Bromage and Shrenk, 1987; Schrenk et al., 1993; Bromage et al., 1995; Bromage and Schrenk, 1995).

Regardless, accessible, published data remain that have not been analyzed using cladistic biogeographical methods and thus offer a decent place to start.

## Chapter 5: Future Paleoanthropological Applications

A pertinent question facing paleoanthropologists remains: how can current paleobiogeographical analytical techniques be applied to paleoanthropology in a meaningful and insightful manner?

As mentioned, the cladistic approach to paleobiogeography has by no means been fully accepted as a legitimate sub-field of historical biogeography (Lieberman, 2000; Upchurch et al., 2002). To reiterate, the major argument against it stems from its use of the fossil record, which by definition is an incomplete chronicle of biotic history. Clearly, taphonomic realities prevent the fossil record from recording all of life's history—most notably, organisms lacking bony skeletons or hard outer shells are essentially unrepresented in fossil deposits. This argument is by no means new—Darwin (1859) devoted all of Chapter Nine in *Origin of Species* to the subject. Nonetheless, as Lieberman (2002) points out, "The fossil record is our one true chronicle of the history of life" (p. 40). In this regard, its value is undeniable and to ignore it when investigating any aspect of natural history is irresponsible. For one, the fossil record undeniably records biotic change across time and is therefore indispensable to the study of historical biogeography.

The majority of arguments against the use of fossils in biogeographical study naturally come from biogeographers only concerned with extant organisms (e.g. Croizat et al., 1974; Nelson and Platnick 1981). Indeed, many researchers' focus on interpreting modern faunal distributions stems from their assumption that the fossil record represents a fundamentally flawed data set. Interestingly, Lieberman (2002) makes the valid point that there is also "imperfection" in the biological record revealed by extant organisms. Lieberman (2002) contends that extinction "prunes" biotic systems such that by solely relying on extant organisms to infer phylogenetic relationships and conduct cladistic analyses, researchers risk compromising

the integrity of their results. In fact, Lieberman (2002) argues that when one compares the "performance" of the fossil record against the extant biota (each in isolation) in cladistic paleobiogeographical studies, the fossil record produces the more accurate results. Admittedly, Lieberman's (2002) "performance test" is a bit tenuous due its reliance on a hypothetical clade of organisms. Furthermore, a legitimate argument can be made that by responding to critics in this manner he exacerbates a needless debate—investigating both extant organisms and fossil specimens as a means to infer historical biogeographic patterns is clearly warranted and required. The inadequacies of each are immutable and it is up to the researcher to identify the impacts such imperfections will have on their specific research goals and potential results.

Another salvo against cladistic analysis in biogeography has been based on methodological grounds with specific regard to the construction of area cladograms and their use in parsimony analyses. Siddall and Perkins (2003) and Siddall (2005) contend that BPA and similar methods are capable of producing multiple, contradictory results for any given set of parameters, arguing that *ad hoc* decisions are inevitably incorporated into any given solution. They conclude that BPA, and other similar methods such as TreeMap and PACT, do not represent "coherent research programs" (Siddall and Perkins, 2003; Siddall, 2005). Granted, this debate is occurring within the field of parasitology from which many of the biogeographical methods were borne and specifically refer to results pertaining to the analysis of host-parasite relationships. Nonetheless, if one is willing to accept the applicability of a method in a manner different than its original intent, one must also give serious treatment to the method's detractors within the discipline from which it came.

Other arguments against cladistic biogeography have come from cladisticians themselves. Hovenkamp (1997) argues that the very process of creating area cladograms erroneously

assumes that geography and taxonomic identity are analogous. Most notably, area cladograms generally have geographic areas repeated across their terminal ends, whereas by methodological definition, the distal ends of true cladograms can each only be occupied by a unique taxonomic unit (Hovenkamp, 1997). As discussed earlier, this strikes at the heart of the notion that area cladograms often convey para- and polyphyletic relationships whereas biological cladograms, by definition, cannot. Additionally, Hovenkamp (1997) contends that only vicariance events can be extracted from biogeographical analysis and therefore it is the relationship between these events, not the geographic areas they serve to define, that should be the focus of biogeographical study. His condemnation of these sorts of analyses is unequivocal: "The uncritical application of phylogenetic methodology to biogeographical analysis results in attempts to order elements that are irrelevant in a pattern which is irrelevant, using criteria that are invalid" (Hovenkamp, 1997:78).

Admittedly, for the purposes of this thesis I can only give cursory treatment to the debate highlighted above. Nonetheless, it must be frankly acknowledged that the analytical techniques within biogeography such as BPA, PACT and TreeMap are not uniformly accepted as legitimate methods within the greater scientific community, and particularly within the cladistic-based disciplines from which they were derived. Needless to say, when articles critical of these methods appear in influential scientific journals such as *Cladistics* are titled, "Bracing for another decade of deception" (Siddall, 2005), one must recognize that these underlying issues are far from settled.

Leaving the methodological debates aside and agreeing that there is value to be gained in the use of cladistic analysis in biogeography, paleoanthropologists must be clear in the limits of applicability as it pertains to hominins.

To reiterate, the studies discussed in the previous chapter all share one potentially confounding assumption that is the crux of debate among paleobiogeographers: a literal interpretation of the fossil record. Namely, by utilizing taxon-history methods, each study treats the absence of taxa within the fossil record as a true absence. Strait and Wood (1999) admirably note this key assumption: "…the absence of evidence is not evidence of absence, but it is necessary to make the assumption [in order to] generate working biogeographic hypotheses" (p. 9196). Noting the difficulty in interpreting the fossil record, Lieberman (2000) adopts a more nuanced stance but nonetheless defends the practice: "As a general rule, absence should be taken as true absence… An approach that treats absence as true absence is justified in regions that have a good fossil record, measured in terms of overall stratigraphic completeness, and have been adequately sampled by paleontologists" (p. 148).

It is difficult to disagree with Lieberman's argument. Undoubtedly, there is a loss of resolution with the rejection of absence data from taxon-history analyses and it is a persuasive notion to suggest that the benefits outweigh the potential costs. Nonetheless, if we are seeking to achieve firm, testable, *repeatable* biogeographic analyses, such assumptions perhaps cannot be allowed. With regard to Lieberman's (2000) statement above, how does one decide whether or not an area has a "good" fossil record, or that is has been "adequately" sampled? Five years ago, few would have argued that the Sterkfontein Valley had not been extensively investigated and yet, in 2008, Matthew Berger discovered a previously unknown species of hominin not quite ten miles away from the famous and well studied hominin sites of Sterkfontein and Swartkrans (Berger et al., 2010). Looking for a moment at the long recognized southern African hominin species *A. africanus* and *P. robustus*, does anyone really assume that because their remains have only been found in sites peppered across northeastern South Africa (with the notable exception

of Taung) that they did not actually inhabit a much wider area? Indeed, many of the paleobiogeographers who disagree with the use of absence data point to the inevitability of scenarios similar to above. While it is a scientific maxim that with new data come new and potentially improved interpretations, it must be recognized that flawed research can often have significant staying power provided it remains unchallenged by peers. If nothing else, recognition of the dangers of including absence data in research must be recognized by those conducting the research, just as Strait and Wood (1999) correctly did. On the other hand, if paleobiogeographers seek more robust interpretations, it may be that they have to sacrifice resolution and seek answers to larger scale questions such as vicariance events specifically related to geological or climatic shifts that affected a broad spectrum of organisms.

One argument in favor of rejecting the use of absence data is found in the methods of Upchuch and Hunn (2001) that were described in Chapter Three. Again, these researchers argue that despite the potential loss of fine scale resolution, biogeographic studies utilizing presence data alone infer benefits missing from the standard cladistic analyses such as BPA. Essentially, Upchurch and Hunn (2001) argue that the two-dimensional area cladograms produced by analyses such as BPA lose the temporal signal that is one of the most valuable and unique qualities of the fossil record. In standard BPA area cladograms, temporally incongruous taxa are placed at the distal ends of the tree and are organized only with regard to their phylogenetic relationship. As an alternative, Upchurch and Hunn (2001) outline a method that creates and compares area cladograms of organisms for specific time slices, essentially creating a three-dimensional analysis of phylogenetic relationships across discrete segments of time. As noted, Upchurch et al. (2002) utilized time slicing to analyze the biogeographic patterns of dinosaurs and found that biogeographical events can be quantifiably teased out in the process.

Another major hurdle to be addressed with regard to cladistic analysis in biogeography, one that is universally acknowledged by supporters and detractors alike, is the assumption that the researcher can obtain competent and accurate phylogenies for the taxa being investigated (Folinsbee et al., 2007; Folinsbee, 2009). This fact stands as the key assumption upon which all cladistic biogeographical analyses, regardless of methodology, are based. As such, the quality of the results is ultimately limited by the quality of the phylogenetic interpretation. As stated, phylogenetic interpretations of hominin taxa are notoriously contentious and thus become problematic in the application of cladistic biogeography to the study of hominin distribution (Strait and Wood, 1999; Foley, 1999).

The fact that the construction of accurate area cladograms relies on an accurate assessment of phylogenetic relationships between species has other implications. Particularly, an operational species concept becomes essential (Lieberman, 2000). How a species is defined remains one of the most contentious debates within the biological sciences (for discussion, see Foley, 1999). For the purposes of cladistic biogeography, particularly in reference to the use of extant and fossil taxa in analyses, it may be that a less rigid species concept must be employed. For one, the biological species concept that has arguably become the most widely accepted is by definition unusable with extinct and fossil taxa. While a working species concept is of utmost importance, it should not stand in the way of future research.

Relevant to biogeographical studies within paleoanthropology, it may be time to reexamine many of the phylogenies that have been historically utilized. Particularly with regard to the bovid studies, many of the original phylogenetic analyses of fossil specimens are now nearly thirty years old (e.g. Vrba, 1985). This does not imply that previously used phylogenies are incorrect, only that methods for inferring phylogenetic relationships have improved in recent

years, namely due to refined techniques in the analysis of morphological and molecular evidence. For example, over the last decade, researchers using molecular analyses have determined that the traditional members of the order Insectivora, in fact, represent a paraphyletic group. Specifically, it is now widely accepted that tenrecs and golden moles, rather than being cast as insectivorans, rightfully belong to the superorder Afrotheria (Stanhope et al., 1998; Asher et al., 2003). Of course, molecular studies cannot speak to all of the phylogenetic ambiguities. Though initially heralded as a solution to all puzzles (as new technological methods often are), molecular biology has also caused considerable confusion and debate, and clouded many of our phylogenetic interpretations (see D'Erchia et al. (1996) for an example of its impact on rodent phylogenetic interpretations). Molecular biology is not a panacea, but for the purposes of biogeographical analysis in paleoanthropology it will be interesting to investigate how the latest interpretations can be incorporated.

Additionally, as cladistic analysis translates taxonomic cladograms into area cladograms, the definitions of discrete geographical regions that can be suitably applied become crucial. Questions of how one goes about accurately defining such regions are scarce in the biogeographical literature. Ideally, improvements in phylogenetic interpretations, as discussed above, will improve our ability to accurately define the geographic regions tethered to specific taxonomic groups.

One final nettlesome aspect that needs to be addressed and is uniquely related to hominin paleobiogeography is cultural adaptation. Arguments abound regarding when, where, and how cultural elements began to become incorporated among our hominin ancestors, but their eventual incorporation remains a fact. If we take the conservative approach and assume that elements of culture begin with the first lithic artifacts presently dated to around 2.5 Ma at Gona (Semaw et

al., 1997), the potentially vital significance to hominin biogeography becomes apparent. Certainly, by the first exodus out of Africa by members of the genus *Homo* we see a dramatic shift in the hominin ecological niche. While I have not touched on the significance of ecological concepts, such as niche theory, to biogeography, there is an argument to be made that biogeographical events, particularly dispersal and dispersion events, are intrinsically taxon specific and thus inherently ecological in nature. The ecological shift seen in hominin history, most strikingly the incorporation of meat into the diet, certainly had implications for the potential biogeographic patterns (Dunbar, 1983). In fact, as mentioned earlier, researchers looking at the relationship between carnivore and hominin biogeographical history interestingly begin to see many similarities between the two after 1.8 Ma (Werdelin and Lewis, 2005). The theoretical underpinnings of ecological niche and its relation to distribution and evolution in general are still being developed, but perhaps represent a complex addition to the study of historical biogeography that may be incorporated in the future (Rosenzweig, 1995, 1999; Lieberman, 2000). Currently a division between historical and ecological methods in biogeography exists for practical reasons, and paleobiogeographers are rightfully reluctant to incorporate aspects of ecological theory into their deep historical analyses. Nonetheless, a certain amount of academic bravery can be an important component of scientific innovation and a synthesis of ecological and historical biogeographical methods, if possible, would be incredibly powerful and enlightening.

One thing remains clear, and that is the fact that when trying to uncover the biogeographical patterns of the hominins, holistic biogeographical methods have rarely been incorporated. Also, in light of new evidence such as *Ardipithecus ramidus* and *A. sediba*, a fundamental reassessment of biogeographical interpretations may be in order. As noted, there exist significant amounts of faunal evidence available to the researcher who is willing to

organize and interpret the disparate collections of data. Likewise, there undoubtedly exists information with regard to other fossil groups that has yet to be analyzed and incorporated into paleoanthropological research.

Lieberman (2001) flatly states that "biogeographic studies of fossil taxa should avoid groups with low diversity and a poor fossil record" (p. 39), a foreboding statement for hominin studies. However, it seems as if the true analytical strength of biogeographical analysis stems from methods that incorporate the widest group of taxa into its interpretations (Andrews, 2007). Just as Croizat et al. (1974) and Nelson and Platnick (1981) propose, the legitimate biogeographical interpretation is to be gained from the distributional evidence with regard to multiple taxa. In this regard, many of the taxa utilized in traditional paleoanthropological research have yet to be analyzed through the lens of cladistic paleobiogeography. The potential for future insight is apparent as the example given below demonstrates.

Interestingly, Denys (1999) worked at the edges of modern paleobiogeographical investigation by separating her micromammal research into three distinct time periods. Utilizing her micromammalian data, we can construct area cladograms and implement an analysis on two of the would-be "time-slices" she provides utilizing the Fitch algorithm (see Appendix 1) to discern events of dispersal and vicariance as described by Lieberman (2000) (Figs. 5.1 and 5.2; Tables 5.1 - 5.4). Indicative of the challenges facing future cladistic analyses, phylogenies of African rodents and insectivores that specifically pertain to the hominin fossil record are difficult to obtain. For the purposes of this exercise, I have utilized the phylogenetic information concerning broad rodent clades provided by Jansa and Weksler (2004). However, their phylogeny does not incorporate all of the species represented in Denys' (1999) fossil data. For

the sake of simplicity, I have limited the analysis to the murinae, acomyinae, and gerbillinae—the clades most significantly represented in both Denys' data and Jansa and Weksler's phylogeny. Also, I have made some gross generalizations with regard to regional affiliations of the taxonomic groups; most notably I have attributed the Namibian and Zambian fossil material into one (artificially) unified region.

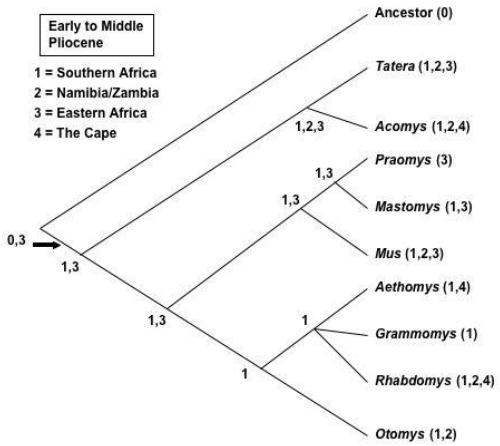



**Figure 5.1.** Area cladogram based on rodent fossil data from Denys (1999) for African hominin sites dated 5 – 2.5 Ma. The Fitch algorithm has been applied in order to obtain the geographical states of the ancestral nodes

**Table 5.1. Vicariance Analysis**

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| South Africa | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | **2** | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Namib/Zamb | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| East Africa | 1 | 1 | 0 | 0 | **2** | 1 | 1 | 1 | 1 | 1 | 1 | **2** | 0 | 0 | 0 | 0 | 0 |
| The Cape | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |

**Table 5.2. Dispersal Analysis**

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Ancestor** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **South Africa** | 0 | **2** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| **Namib/Zamb** | 0 | 0 | **2** | 1 | 1 | 0 | 0 | **2** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **2** | **2** |
| **East Africa** | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| **The Cape** | 0 | 0 | 0 | 0 | **2** | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | **2** | 0 | **2** | 0 |

**Tables 5.1 and 5.2.** Two data matrices based on Figure 5.1 utilizing the coding procedures described by Lieberman and Eldredge (1996). Table 5.1 is weighted to identify events of vicariance, denoted by a "2" in the matrix cells. Table 5.2 is weighted to identify dispersal events.

With this partial analysis of Denys' (1999) data for hominin fossil sites dating from the Early to Middle Pliocene (5 -2.5 Ma), vicariance and dispersal events clearly emerge. The analysis above suggests that an initial dispersal event occurred shortly after this related group of organisms diverged from its ancestor (a "2" in column 2, table 5.2). Dispersal events were also responsible for the emergence of the genera *Otomys, Rhabdomys, Aethomys,* and *Mus,* as well as for the ancestral species of the sister taxa, *Tatera and Acomys.*

Similarly, Figure 5.2 and Tables 5.3 and 5.4 below apply the identical analysis to Denys' (1999) data from sites dated from the Late Pliocene to Early Pleistocene (2.4 – 1 Ma).

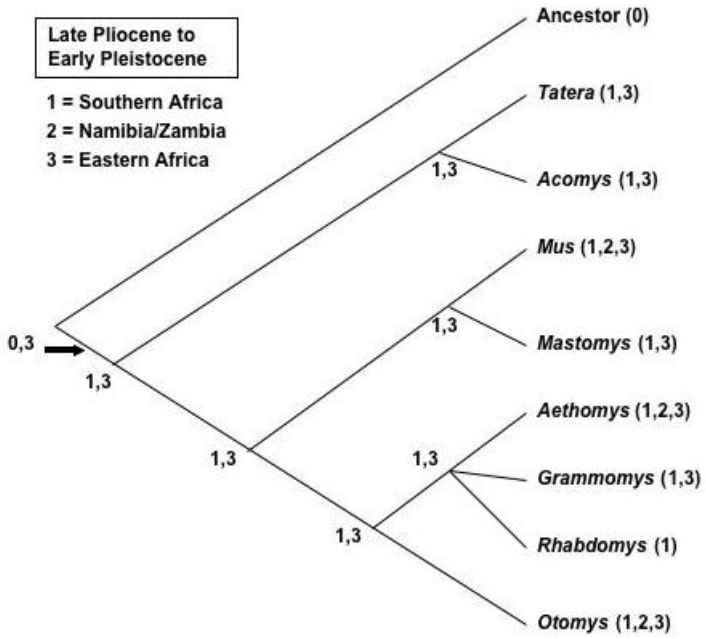



**Figure 5.2.** Area cladogram generated after the application of the Fitch algorithm for hominin sites dated from the late Pliocene to early Pleistocene (2.4 – 1 Ma).

**Table 5.3. Vicariance Analysis**

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| South Africa | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | **2** | 1 |
| Namib/Zamb | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| East Africa | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

**Table 5.4. Dispersal Analysis**

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| South Africa | 0 | **2** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Namib/Zamb | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **2** | 0 | 0 | 0 | **2** | 0 | 0 | **2** |
| East Africa | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |

**Tables 5.3 and 5.4.** Two data matrices based on Figure 5.2 utilizing the coding procedures described by Lieberman and Eldredge (1996). Table 5.3 is weighted to identify events of vicariance, denoted by a "2" in the matrix cells. Table 5.4 is weighted to identify dispersal events.

From the analysis of the Late Pliocene to Early Pleistocene sites, one vicariance event and four dispersal events emerge. A dispersal event is responsible for the separation of the listed taxa from the ancestral species, denoted by at "2" in the column corresponding to node two in

Table 5.4. Dispersal events are also attributed to the emergence of the genera *Otomys, Aethomys,* and *Mus*. The lone vicariance event detected occurred with the emergence of *Rhabdomys*.

Clearly, the time periods analyzed above present obvious incongruence. Both depict a dispersal event at the stem of their trees (node 2) and thus imply a temporal disconnect. In traditional BPA analysis, the time periods would not be separated as they are here, and all of the fossil data would be combined into a single cladogram. However, agreeing with Upchurch et al (2002), in doing so one loses the temporal clarity that is provided by the fossil record. On the other hand, I have ignored Upchurch and Hunn's (2001) admonition against treating the absence of data as true absence, as I have utilized the Fitch algorithm in order to determine the character states of the ancestral nodes. Needless to say, Lieberman (2001), among others, would deem such an assumption appropriate despite my inclination to argue otherwise.

Future cladistic analyses of Denys' (1999) research will potentially incorporate her entire data set for each time slice while accounting for presence data only. At this time I lack the comprehensive phylogeny to perform such an analysis, not to mention the fact that I am unfamiliar with the necessary software to perform such a comprehensive investigation. As such, these analyses are for demonstrational purposes only and should not be utilized to draw any coherent conclusions about African rodent biogeography. They merely serve to illustrate what is potentially achieved by the application of new methods to readily available data, and should be effectively regarded as hypothetical.

Clearly, the fossil record that pertains directly to hominins is both abundant and well documented and provides an accessible database from which to base many, if not all of the current cladistic biogeographical methods. As stated, one of the many hurdles is the acceptance of a competent phylogeny for the desired taxonomic groups and a discrete understanding of the

areas occupied by each taxon. Needless to say, the work to be done is both complex and challenging and will require collaboration with scientists in multiple disciplines in order to obtain informative results.

## Chapter 6: Conclusion

Biogeography has much to say about the complexities of life on earth and as such can make significant contributions to a wide range of natural sciences. For paleoanthropologists seeking to reconstruct the evolutionary events of our hominin past, biogeographical analyses are indispensable. However, the value of the biogeographical interpretation is only as good as the rigor and care with which scientists discern and apply the relevant methods and theories.

As has been discussed, the broad dissection of biogeography into historical and ecological inquiries suggests that those seeking to understand the ancient past, paleobiogeographers, are precluded from fine scale ecological interpretations. However, as biogeography gains insight from other disciplines working in tandem, particularly the fields of molecular biology and genetics, the barriers between the ecological and historical approaches may begin to erode. Hard scientific evidence from the chemical history written in cells, combined with continuing refinements of ecological theories may mean that in the not-so-distant future, paleobiogeographical patterns may be able to be reconstructed at finer scales. While this may sound fanciful, it is worth bearing in mind that only two decades ago, consensus held that paleobiogeographical studies incorporating the fossil record were essentially a fool's errand (Lieberman, 2000).

For future hominin related biogeographical studies, a new range of possibilities is emerging. Dating techniques used to determine the ages of fossil hominins and associated fauna are continuing to improve. Even in the notoriously jumbled stratigraphy of South African cave sites, U-Pb dating has enabled researchers to attach dates to fossil finds that are nearly on par with the precision dates more closely associated with East African sites (Pickering and Kramers, 2010). Also, new fossil discoveries continue to be made, despite the past prognostications by

some prominent anthropologists (see White, 2000). The recent discoveries and publications of material related to *Ardipithecus ramidus* (White et al., 1994; 2009), *Sahelanthropus tchadensis* (Brunet et al., 2002), *and Australopithecus sediba* (Berger et al., 2010) (to name a few) have reminded the field that our understanding of the hominin past, though unclear and incomplete, will continue to improve.

As discussed, ample sets of data already exist that are well suited to a modern biogeographical interpretation of the hominin fossil record. Past investigations into bovid, rodent, suid, and carnivore evolutionary histories (among others) contain troves of evidence that are well suited to novel manipulation and interpretation. One can only wonder how many boxes and jars of fossil material lie in museums, waiting for the dedicated scientist to rediscover their worth and find new ways to incorporate their valuable historical insight into our holistic understanding of the past. A sturdy history of paleoecological research exists in paleoanthropology based on climatic, morphological, and isotopic evidence. It may be that paleoanthropologists, because of their need to incorporate disparate lines of evidence into their research are in a unique position to forge new methodological syntheses for biogeographical interpretations (see Reed and Bidner, 2004). In fact, it may be the case that paleoanthropologists can take the lead in the development of new biogeographical techniques, testing new methods that incorporate some of the ecological theories and models that have long been regarded as solely applicable to modern biotic systems.

One interesting idea would be to utilize a new transformation of cladogram data. Just as Nelson and Platnick (1981) substituted geographic areas for taxa on traditional cladograms, perhaps some other taxon-specific characteristic can be analyzed via a cladogram tree. Reed (1997) developed a taxon-free means to interpret faunal evidence, suggesting that by examining

the ecological adaptations shared by multiple organisms (ecomorphologies) a broader understanding of environmental change can be gleaned. If we were to replace the taxa on a cladogram with the different character states of ecomorphological adaptation that each taxon exhibits, might we be able to understand the spatial relationship between adaptations within a clade of organisms? Could we then reconstruct the environmental transitions of the organisms through time? If we were to relate this to the biogeographical area cladogram analyses we could potentially discern not just geographical transitions, but the environmental characteristics of each transfer point. Interestingly, Foley (1999) has argued that the progression of ecomorphological, evolutionary transitions within a taxon through time invariably runs from forest adaptations to adaptations to more arid climes—never in the reverse. Some form of "ecomorph cladogram" might lend insight into his hypothesis.

While the biogeographical literature as it directly pertains to paleoanthropology has been scattered and incongruous, researchers such as Folinsbee (2009) are turning a fresh and dedicated eye to updating the paleoanthropologist's biogeographical toolkit. The most conspicuous task that lies ahead for those wishing to pioneer new research is grappling with the current phylogenetic interpretations of the fauna upon which future paleobiogeographical studies will inevitably be based. At a deeper theoretical level, it may also be time for paleoanthropologists to abandon the dogmatic separation of eastern and southern Africa into two distinct areas of study. While there is ample evidence to support the biotic separation of the two regions for much of hominin evolutionary history, there nonetheless remain important interactions between the two that pertain specifically to our evolutionary past. Admirably, scientists such as Turner and Wood (1993) and Wood and Strait (1999) )among others) have sought to bridge the East-South research

divide with their efforts to discern the spatio-temporal relationship between the paranthropines. Yet, far too many researchers remain focused on one area at the exclusion of the other.

The application of biogeographical methods can help integrate our evidence from eastern Africa, southern Africa, and beyond, and biogeography deserves a prominent position in future paleoanthropological research. Its insights will undoubtedly help paleoanthropologists edge closer to a comprehensive and more accurate understanding of the unique combination of events that lead to the emergence of *Homo sapiens*.

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## Appendix 1: The Fitch Algorithm

The Fitch algorithm (Fitch, 1971) as described by Lieberman (2000:121-122), including the specific modifications of nomenclature made by Lieberman and Eldredge (1996) and Lieberman (1997) in order to make it more accessible to biogeographers.

***Phase 1.*** (The Preliminary Phase): The geographic states at this point should be at the tips of the species tree, having replaced the names of the taxa; the method then proceeds from the descendants (the terminal taxa) to the ancestors, starting with those that are immediately ancestral to the terminal taxa. The ancestor is assigned geographic states, based on those that are present in its immediate descendants. If the descendants share no geographic states in common, then all of the geographic states are utilized, which is referred to as taking the union of these states. If they share some or all of their states in common, then only the states held in common are utilized in the ancestral reconstruction, which is known as taking the intersection of these states. The method then proceeds backward toward the base of the tree, which is the last common ancestor of the entire clade. This preliminary phase is followed by a six-step second phase that is employed in the following sequence and can be described as a sort of flowchart. Unlike the first phase, which proceeded from top to bottom (descendants to ancestors), the second phase proceeds from bottom to top, or from basal ancestors to more derived ancestors and descendants.

***Phase 2. (i)*** if an ancestral node has all of the geographic occurrences present in its immediate ancestor got to *ii*, otherwise go to *iii*; ***(ii)*** delete all of the geographic occurrences not present in its immediate ancestor and go to *vi*; ***(iii)*** if in the preliminary phase the union of the states was taken, go to *iv*, otherwise go to *v*; ***(iv)*** add to the ancestral node any states that are present in its immediate ancestor that were not present after the preliminary phase and go to *vi*; ***(v)*** add to the ancestral node any states that are present in the final set of the immediate ancestor and in at least one of the immediately descendant sets and go to *vi*; ***(vi)*** the final phase is complete; go to the next ancestral node up the tree and return to *i*.